THE
NEW PHYTOLOGIST

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TOWARDS AN IDEAL BOTANICAL CURRICULUM.

PART III.[1]

ADVANCED UNIVERSITY TEACHING.

THE conditions governing advanced botanical work, such as should lead up to an Honours degree at a University, are, or should be, very different from those which obtain in the elementary part of a botanical curriculum. The time has definitely passed when a candidate for such a degree can hope to have even a decently competent knowledge of the whole field covered by the modern science of Botany, and the same is true, we imagine, of all other branches of science. It may have been possible twenty or perhaps even ten years ago; it is certainly impossible to day, and will become more obviously hopeless with every year that sees the continuance of the enormously increased and increasing activity in every branch of science. The sooner this is explicitly recognised the better for both teachers and students. The attempt to "cover the ground" which is still made in certain quarters, can only result in unmitigated "cram," and that worst of its results, the utter weariness of a mind which has lost all its freshness in the constant effort to store up for examination purposes an endless series of details. It is true that there is a type of mind which does attain extraordinary success in this kind of occupation. It is the type to which some of the most brilliant "examinees" under the old system belong, and there is no need to disparage the peculiar intellectual powers that characterise it. Properly employed, this kind of capacity for the absorption and mental pigeon-holing of detailed facts is of the greatest use. But it must be insisted that the mere endless repetition of this process is in no sense a training in science—the student would be almost as usefully employed in acquiring an exhaustive knowledge of the various issues of postage stamps in the

[1] Parts I. and II. appeared in June and October, 1902.

different countries of the world—and the obtaining of a "brilliant" degree in this way can be no test whatever of a real scientific education. Further, the system of teaching and examination which puts a premium on this kind of faculty, simply tends to destroy the natural powers of the average student who does not possess it, and to create in his mind a kind of dreary chaos of miscellaneous and imperfectly assimilated information, so that—to put the matter on its lowest level—he would never get a degree at all if it were not for the disgracefully low pass standard which obtains in certain degree-examinations. If then it be admitted—and it can hardly be denied—that it is impossible to teach properly the whole subject-matter of modern botany, or of any other branch of science, during the period of the curriculum (say two years) of the advanced student, the question at once arises, how is the subject-matter to be limited. The answer seems to be that, given a sound elementary training of the sort indicated in the last article, it does not much matter *what* s taught afterwards, provided it is taught on the right lines and by a thoroughly competent person. Supposing a man to have a good elementary knowledge of the outlines of his subject, he may be afterwards trained in some branch of Plant-Physiology, in part of Morphology, or of Systematic Botany, and may become a sound botanist in one of these fields; it is out of the question that he can become so in all of them.

Before proceeding to discuss the methods of training more in detail, it will be well to consider a practical objection which may be raised at this point. It may be urged, and with some force, that we are leaving out of account the ordinary object with which a man or woman enters for a science degree, the desire to qualify him or herself for the teaching profession. No doubt, it may be said, your scientific investigator is best taught in the way you indicate, but how shall it profit a science-master in a secondary school to have been trained as an accomplished systematist, or as an expert in the physiological chemistry of plants, with only the barest knowledge of the general subject he will have to teach to his boys. The lines on which we should answer such an objection would be somewhat as follows. A really good elementary course in botany (and the same applies to any branch of science) should give the intelligent student such a vital idea of the ground-work of his subject that he could readily build up his knowledge in any direction he chose. A man who after taking his degree sets out to teach a branch of science must necessarily, to some extent, shape the whole matter

afresh in his mind before he can actually begin to teach with effect; he must, that is, make up his own mind in what directions his knowledge has to be expanded and strengthened, and have the means to do what is needed in these directions for himself; he cannot dole out to his unfortunate pupils the contents of "cram" lecture note-books: and he should be in the best position to do his own remoulding if he has gained the right perspective of the whole subject from a really good elementary course. And now if to this he has been able to add the experience, the wider and deeper views of one or more branches of his subject, gained from a real training in the right sort of advanced work, he will inevitably teach with the added power and conviction that are brought by a really thorough, living, and fundamental knowledge, even of a small part of a subject. This of course is only another way of saying that a genuine scientific training makes a better teacher of a man than the most exhaustive course of instruction in the mere "end-results" of other people's work; a proposition which will appear sufficiently obvious to some of our readers, but which has certainly not been a guiding maxim in framing many of the current degree-examination systems.

What then, is the exact nature of the ideal advanced curriculum in which students should be trained, preparatory to taking an honours degree in botany? We believe that such a curriculum can only be properly conducted by specialists in various branches ot the science, giving independent courses on their own subjects. Each should aim in the first place at giving the students an exact idea of the current state of the particular department in question. The teacher should begin by building up the subject on its natural foundations, relating it to adjacent subject matter, "placing" it in fact, and too much attention cannot be paid to the careful logical enunciation of the fundamental ideas concerned. The subject should be developed in its "état actuel," established principles being related to those which are still in the hypothetical stage, and to the nearer problems as yet unsolved, principles should be illustrated by observation or experiment in the laboratory or in the field, and at the same time every opportunity should be taken of getting the students themselves to push our knowledge a little further forward. It is only by thus leading a student, so to speak, along the border-line between the known and the unknown, that the full meaning of the scientific method in its actual working can be brought home to him, and only when this has been done, when he has lived so to speak in

that stimulating atmosphere of unsolved or only partially solved problems, that he can be said to have had a scientific training worthy of the name.

It is obvious that a course of the kind we have sketched can only be conducted by a specialist, who himself will usually have engaged in research on the special part of the subject he is teaching. In a well-equipped University there will naturally be a number of such specialists at work on original investigation, and available for advanced teaching.

Each course should last one or perhaps two terms, according to the nature and scope of the particular field, and during this period the teacher should devote a great part, and the student the whole of his time to the subject. What is wanted is nothing less than "saturation" in the subject. As it seems now to be generally agreed that a candidate for an Honours degree in natural science should only be required to take one of its chief branches, at any rate that he should devote very much the greater part of his time to one such branch, it would be possible in this way for the student to take up four or five different branches of botany, and these should be so chosen as to give him some training, at least, in widely different fields. Thus it might be insisted that a man should go through at least one course which took him into the field, at least one which took him into the physiological laboratory, and so on. Supposing as might be the case in a large University the number of specialists available for teaching were large enough, the student might also be allowed a certain choice of subjects. The courses should be so arranged that an advanced teacher should only have to teach about one third of his time, say for one term in three, and the demand for a large part of his days during that term could then be made with justice and propriety, while he would be saved from that worst of the diseases incident to the teaching profession, the staleness and flatness consequent on teaching much while investigating and thinking little. These advanced teachers should be the holders of adequately but not necessarily very highly endowed posts—posts, that is, the emoluments of which should amount to a living wage, but should not be anything like so great as those of the chief Professor.

The examinations, it need scarcely be said, would on this system, be strictly adapted to the courses which a student had actually been through. Each would be held soon after the end of a course. It would be absolutely necessary that the teacher should examine in each case, for the simple reason that *no one else would be*

in a position to do it, but there could be no objection, indeed it would be an advantage, that a competent independent botanist should be associated with the examiner as a sort of moderator, to modify any eccentricities which might appear in his method of conducting the examination. The standard might be made as high as was thought fit—in the opinion of the present writer the higher, in reason, the better; we do not want men with the Honours degrees in science of our great Universities who have proved themselves unable to take the fullest advantage of the opportunities they would have under such a system as we have outlined. What has been written seems to apply equally well to any branch of natural science, though it is the result of experience gained mainly by the learning and teaching of Botany.

Let us now therefore briefly summarise the scientific curriculum which would obtain in our ideal University.

For the first two years after matriculation the student of natural science would be engaged in elementary work. He would attend two courses in each year, the first year being compulsorily devoted to chemistry and physics. In his second year he would have a choice of two among the other branches of natural science. The regular set work would be held on the mornings of the days only, but students would always be encouraged to come in the afternoons also, and there would always be a demonstrator ready to give any assistance in his power. The lectures would be delivered, or the "heuristic" class conducted, by the chief Professor himself.

At the end of each year an examination would be held at which each candidate would take the two subjects he had been working at during the year. The pass standard should not be lower than 50°/₀ of the marks obtainable. On passing the second of these examinations the student might well be granted a Pass degree in Science. If he aspired to an Honours degree he would go directly during his third year into the class of one of the advanced teachers of his chosen subject, which would take all his time for one or two terms, and by the end of his fourth year, when he would have taken say four courses in his chosen (main) subject, and one in a subsidiary subject, he would, if he had passed all his examinations, be entitled to his degree. If he failed in any of these—or in other words if he failed to give satisfactory evidence of solid and successful work—he would have to try again till he had obtained the proper number of certificates.

Such a scheme is certainly based on sound lines, and it seems

simple enough and practical enough; the only criticism that suggests itself is that it would only be practicable (at least in its entirety) in a large and well-endowed University. That is no doubt true. Real scientific education is expensive, very expensive—it is no use shutting our eyes to the fact; and it must be centralised to be efficient. But it is at least well to have an understanding as to what is desirable, and as to the direction in which our Universities, old and new, should aim.

MISCELLANEOUS NOTES.

The "Botanisches Centralblatt."

THE "Centralblatt" has now completed its first year of publication under the auspices of the "Association Internationale des Botanistes," and it may not be out of place to offer a few criticisms on the two half-yearly volumes published under the new régime.

The attempt to notice practically all botanical publications would be most praiseworthy if it were at all possible to carry out, but at present it results in a considerable amount of space being devoted to records (with perhaps a line of description to each) of a large number of small papers or notes of very limited interest, while notice of more important work has been in some cases neglected, or at any rate seriously delayed. Then again the lengths of the different notices are by no means proportional in all cases to the relative importance (or even to the relative length) of the works reviewed. These defects are of course due to the different conceptions of their duties entertained by the various special editors. While some endeavour to include all published matter relating in any way to their department of Botany, others clearly confine themselves within much narrower limits. It would be better if rules could be laid down which would secure more uniformity of treatment.

These remarks are by no means made in any hostile spirit. The enormous difficulties which the general editor must experience in dealing with the reviews sent in by sub-editors from many different

countries spread over half the world are sufficiently obvious; but still there can be little doubt that more central direction and organisation is really wanted. Misprints are rather distressingly common, and it is clear that very many simply result from ignorance of the various languages on the part of the compositors. Probably this could be remedied by employing a printer's reader who had a working knowledge of the three languages in which the reviews are written.

The continuous paging of the lists of new literature, so that the whole of this matter comes together when the volume is bound, will be very useful in facilitating reference to back-volumes. The same principle might well be adopted within the different subdivisions under which the "Referate" are arranged in each number, so that, for instance, all the notices of papers on Fungi throughout the volume would be continuously paged and come together in the bound volume.

Meanwhile the "Association Internationale" and particularly the Editor-in-Chief, Dr. Lotsy, must be congratulated on having established and begun to carry on the "Centralblatt" on an international basis. The result has already been that numbers of papers are now noticed which were necessarily neglected under the old régime, and the publication is certainly more valuable than ever.

The old "Beihefte," now entirely devoted to original papers, under the editorship of Drs. Uhlworm and Kohl, is published by Fischer, of Jena, and is very well got up, with most admirable plates. Papers are published in the "Beihefte" in English or French, as well as in German, so that this periodical also partakes of the international character. It may be recommended to English authors who find the home journals inconveniently crowded. One sensible feature of the "Beihefte" is their appearance in "zwanglosen Hefte," *i.e.* at no fixed times, but as soon as enough papers are ready to make up a suitable size. In this way rapid publication is assured if there is a good supply of papers, the only drawback being that subscribers may find the annual cost of the periodical mount up rather alarmingly. What is really wanted is a scheme by which subscribers to a periodical entirely composed of original papers could obtain only what they wanted and would not have to pay for what they did not want. There are, of course, obvious and serious financial difficulties involved, but it is probable that these could be surmounted after a little consideration of the problem.

The Late Professor Celakovsky.

By the death of Professor Celakovsky, of Prag, which occurred at the end of November, we lose probably the most brilliant plant-morphologist of the latter end of the nineteenth century. His work extended over a very wide field, and was always characterised by ingenuity, clearness, and logical accuracy in working out the ideas involved. In some of the harder problems which he essayed, he did not carry complete conviction to all of his readers, but much of his work stands out well above that of most of his contemporaries for real insight into the factors governing the history of form among plants. To mention two conspicuous examples: his early work on the conception of antithetic alternation of generations was a most striking advance on previous ideas, and has proved itself extraordinarily fruitful since; while his "Reductionsgesetz der Blüthen," published in 1894, a most luminous and, in parts, a very lively work, is certainly the most important contribution to floral morphology of the last decade of the nineteenth century. Celakovsky's repudiation of the notion that the history of development of an organ in the individual is an infallible guide to its ancestral history is particularly vigorous and of the most far-reaching importance.

Methods of Preserving Museum Specimens.

The great beauty of the botanical specimens exhibited in the Museum of the Royal Botanic Garden of Edinburgh is well-known to all botanists who have visited the Garden. Mr. H. F. Tagg, who is largely responsible for this work, has recently published a little pamphlet on "Museum-Methods," which ought to be of great use to all those who have similar specimens to prepare. Mr. Tagg treats his subject systematically under the heads of the different liquid media used for preservation of the objects, so that information on the different methods is very readily found.

It is of interest to notice that Mr. Tagg finds "drying the plant the only method at all satisfactory for preserving the colours of plants," while in the use of liquid media for the preservation of *form*, he very properly distinguishes between the preservation of the individual organs, and the preservation of what he calls the "lie" of the organs. The last point does not always receive the attention it should in the mounting of museum specimens.

The general conclusion reached is that 90°/₀ alcohol is still by far the most satisfactory medium for preserving herbaceous structures, and particularly for preserving the "lie" of the parts. Aqueous media make the specimens too flaccid, so that the natural relationship of the parts is not preserved. It is not safe to use alcohol for this purpose of a lower strength than 90°/₀, but for succulent organs lower strengths are very useful to prevent the wrinkling of the surface which results if they are placed directly in 90°/₀. Such specimens should be placed in 30°/₀ and slowly graded up to the higher percentages. Exposing the jar containing the specimen when first placed in alcohol to strong sunlight is recommended as greatly facilitating the bleaching process and preventing the formation of discolouring decomposition products, which may in some cases stain the specimen very badly if it is put in the dark in a small quantity of alcohol immediately upon being killed.

None of the aqueous preservative fluids are spoken of very highly, they all tend to render specimens flaccid, and they do not really preserve the natural colours well. In the case of formalin, "Red and yellow colours are retained longer than blue, but even red—the colour which has proved most permanent—ultimately fades or gives place to a brown if the jar containing the specimen is exposed to the light." And again, "formalin does not appear to extract chlorophyll, neither does it preserve the green colour, but exposed even to diffused light the chlorophyll is decomposed and the specimen assumes a dull brownish colour, or may, finally, be bleached quite white." Solutions of formalin weaker than 10°/₀ (*i.e.* 4°/₀ formaldehyde) do not cause such rapid fading as the stronger ones, but on the other hand they permit the growth of moulds. Further, not only is formaldehyde very volatile, so that the fluid seriously weakens unless the jars are very securely sealed, but it appears that changes and decompositions may take place in it in the presence of organic substances. The other aqueous preservatives are not very much to be commended for strictly museum purposes.

Other topics dealt with are methods of drying, and poisoning dried specimens, and the methods of bleaching specimens preserved in alcohol. Many, as is of course the common experience, bleach readily in 90°/₀ alcohol; others do not, or even darken in alcohol. In

the latter case it is best if possible to prevent darkening by very rapid killing, *e.g.* in boiling water or boiling alcohol, or by bleaching in acid alcohol (90°/₀ alcohol with 2°/₀ by volume of HCl) in sunlight before transference to the alcohol in which they are to remain. If this has not been done, and the specimens are already darkened in alcohol, they can be bleached in acid alcohol in the same way, but this is not always effective.

Photoxylin (which can be obtained from Grübler of Leipsig) is strongly recommended as a cement for attaching light objects preserved in strong spirit, while gelatine has to be used for heavy specimens. For coloured pointers to indicate parts in labelling specimens preserved in liquid media, an ingenious use is made of capillary tubes filled with coloured plaster.

The paper is illustrated by two excellent photographs, one of a dry object—fruit of sycamore; the other wet—the fruit of *Phallus impudicus*, each showing a set of specimens fully dissected and labelled to illustrate structure.

ON THE CONDITIONS OF TELEUTOSPORE GERMINATION AND OF SPORIDIA FORMATION IN THE UREDINEÆ,

By Vernon H. Blackman, M.A.,

Assistant, Department of Botany, British Museum.

[With Figs. 4-6 on Plate I.]

As is well known the germ-tube produced by the germination of the teleutospores of the Uredineæ is usually described as of *limited growth*. Such a description, however, is not altogether satisfactory, for since all the Uredineæ are, as far as is known, obligate parasites at all stages of development, the growth outside the tissue of the host of any germ-tube or hypha must necessarily be strictly limited by the amount of reserve material at its disposal. In the case of the teleutospores the term is, however, used in reference to the fact that under the usual conditions the germ-tube after developing to a certain extent ceases to grow, and gives origin to the four sporidia-bearing cells, becoming, in fact, so-called *promycelium*:

When, however, one compares the various published figures of teleutospore germination (*e.g.* those of Tulasne, De Bary, Plowright and Sappin–Trouffy), it is clear that the limit of growth is apparently very different in different cases. In some the promycelium is of very considerable length, and only the apical portion has become divided into the sporidia bearing-cells, the lower portion being merely an empty hollow tube (cf., the figures of Sachs and Tulasne for *Puccinia graminis*, reproduced in most text-books; *Gymnosporangium*, Tulasne, pl. x., fig. 7; *Triphragmium*, Plowright, pl. iv., fig. 6.) In other cases the promycelium is exceedingly short, so that it is reduced to little or nothing more than the four characteristic cells (cf. *Puccinia graminis*, Massee, fig. 65; *Phragmidium rubi*, Tulasne, pl. ix., fig. 15, Plowright, pl. iv., fig. 8; Sappin-Trouffy, fig. 50; *Gymnosporangium*, Tulasne, pl. x., fig. 6; *Cronartium*, Tulasne, pl. xi., figs. 16-18.)

If the differences in length of the promycelium were confined to teleutospores of different species they might be accounted for by specific differences of development; but variations in the length of the promycelium quite as great are to observed in the teleutospores of one and the same species (cf. the figures of *Puccinia graminis* and *Gymnosporangium* mentioned above), and even in the individual cells of a single compound teleutospore (cf. Plowright, pl. iv., fig. 6.) Variations such as these can only be explained as a result either of varying external conditions, or of individual spore (or cell) differences.

The external conditions necessary for the germination of the telentospores and for sporidia formation are, as is well known, moisture, and a certain degree of temperature. According to most observers the moisture can be supplied either in the form of water or of damp air; but, apart from this, there is very little knowledge as to the exact conditions necessary for the two processes.

In the spring of last year some observations were made on the germination of teleutospores of *Uromyces fabae*, De Bary, *Puccinia graminis*, Pers, and *Phragmidium rubi*, Wint. (the teleutospores of all three requiring a winter's rest before germination), which show that sporidia formation must be sharply distinguished from germination in relation to external conditions, and that the variation in length of the promycelium is due to the varying action of a definite external factor.

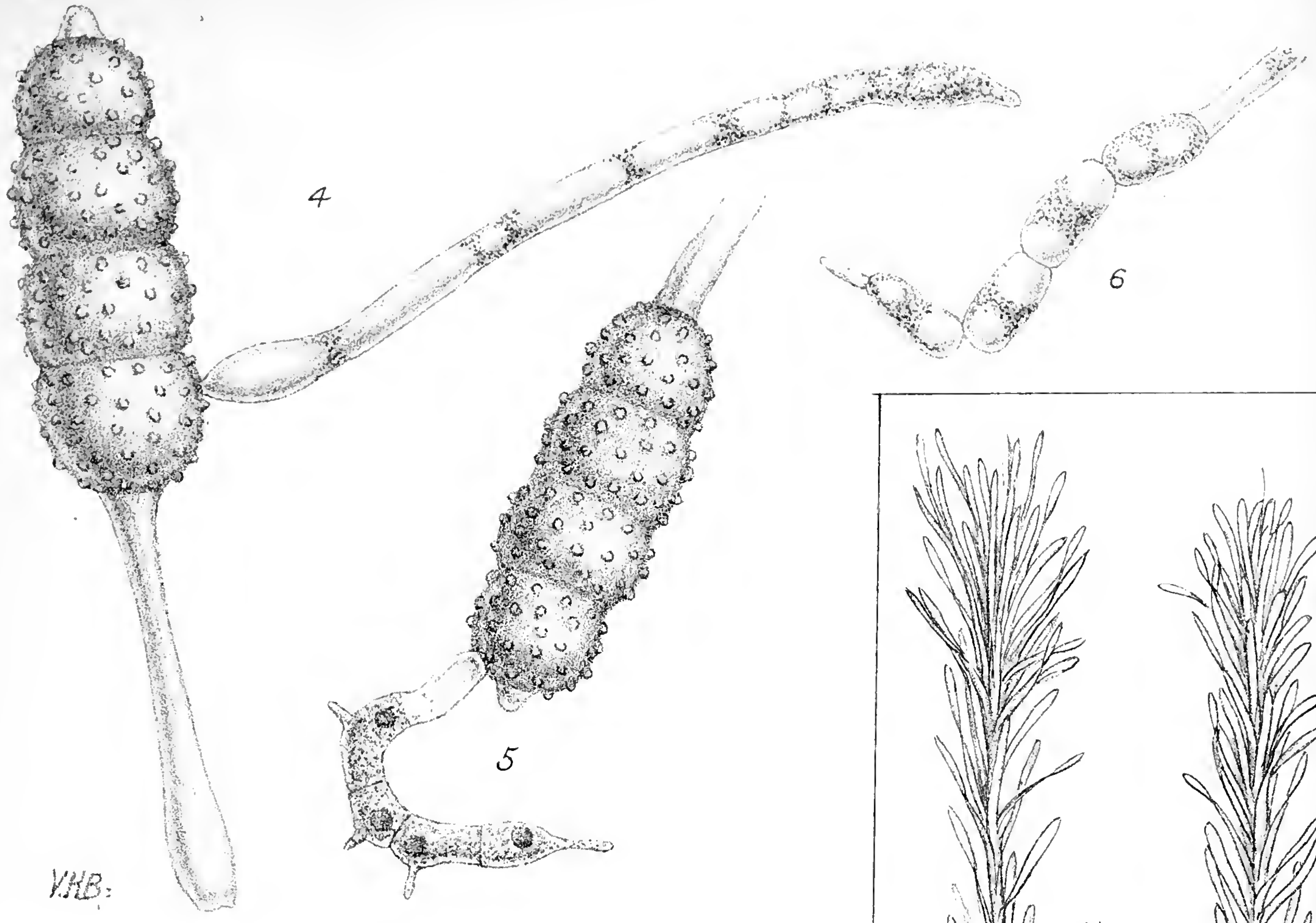
The spores were sown partly in hanging drops, and in part *over* water in Petri dishes so that the spores themselves were

surrounded by a moist atmosphere. Those sown in the hanging drops germinated after some delay, but most of the tubes produced formed no sporidia, but grew to a considerable length in the water without showing the least signs of the formation of transverse walls. As the tube increased in length the protoplasm collected at the apex, the cavity behind being left almost empty. A few of the tubes, however, by continued growth reached the free air outside the drop, when their growth soon stopped and the portion in the air became divided into the usual four sporidia-bearing cells. Only a small proportion of the tubes produced in the hanging drop succeeded in developing sporidia, and there was no evidence that they were positively chemotactic towards oxygen.

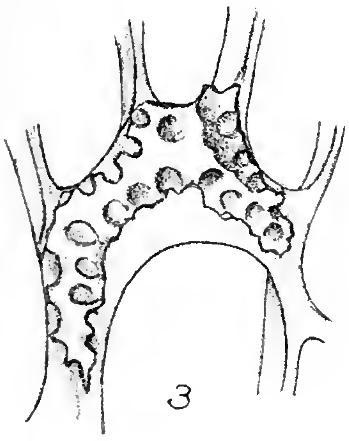
The spores sown in the moist air germinated more readily than those in the drop cultures, but the germ-tubes so produced were very short and formed sporidia almost immediately, so that the promycelium consisted of little more than the four sterigma-bearing cells. In pl. I., fig. 4, there is shown a compound teleutospore of *Phragmidium rubi*, two of the cells of which have germinated in a hanging drop. The lower germ-tube has reached a very considerable length, but there is no sign of sporidia formation; the protoplasm has collected mainly at the apex. Many of the germ-tubes were very much longer, but unless they reached the air, they never became divided into sporidia-bearing cells. In fig. 5 a similar teleutospore is shown, which has germinated in moist air. The promycelium is very short, division into four cells has taken place, and the sterigmata are already formed.[1]

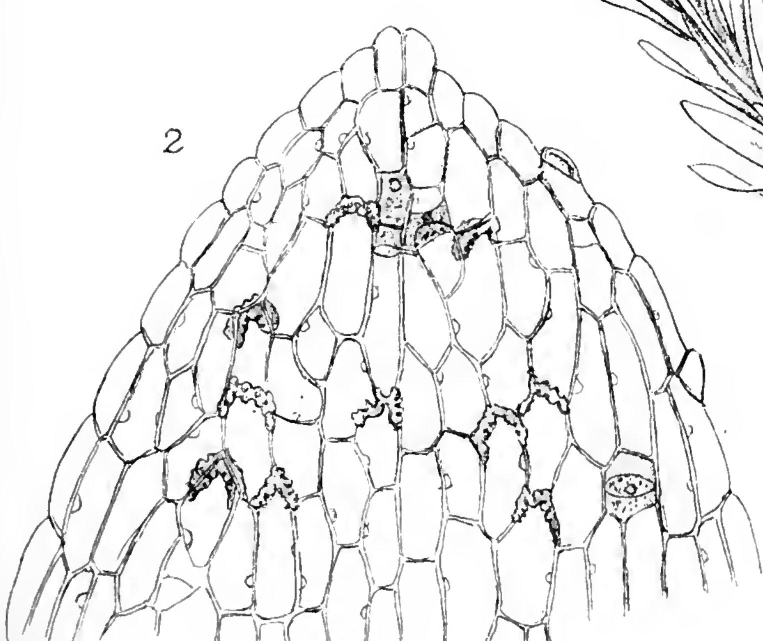
It is clear from the two sets of observations that, in the forms under consideration, the *submerged* germ tube or promycelium is incapable of sporidia formation, but that its growth in length is only limited by the reserve material at its command. Sporidia formation however takes place directly the tube reaches the air, and if this condition is present from the beginning of germination, growth in length is of very short duration and the promycelium becomes reduced to little or nothing more than the characteristic four cells.

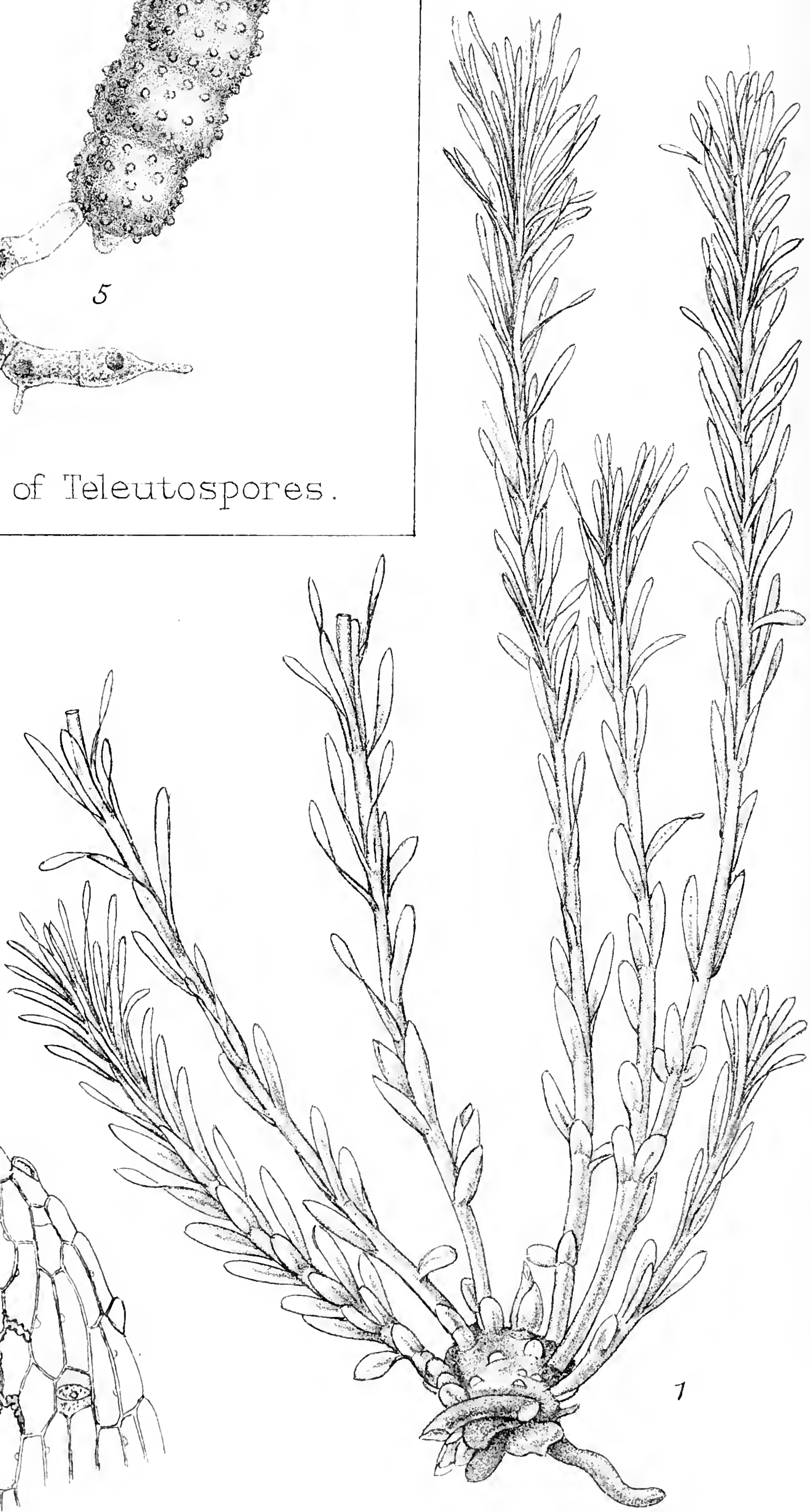
[1] Whether the existence, even in the case of the spores grown in moist air, of a small portion of promycelium which forms no part of the sporidia-bearing cells (as in fig. 5) is a normal phenomenon or is to be explained by the presence of a thin layer of water deposited from the air upon the spore wall, could not be ascertained. The fact that in the figure of *P. rubi* given by Sappin-Trouffy this stalk-like portion is till more reduced, and in the figure of *Cronartium* given by Tulasne (loc. cit.) it seems to be entirely absent, would suggest that the latter explanation is the probable one.



Germination of Teleutospores.







G. L. del. Highley lith. et imp.

Tristicha alternifolia Tul.

As these conclusions are based on observations made on three genera of the Uredineae and as they explain completely the divergent results obtained generally by other observers, there seems very little doubt that they hold good for all the members of the group. The varying lengths of the promycelium hitherto described would then be accounted for by the varying thickness of the stratum of water through which, in the different experiments, the hyphae had to grow before reaching the free air.

As the sporidia depend largely on the wind for their dispersal, the close connection between their formation and the presence of free air is not unexpected, especially as such a relation has been exactly described for the sporidia formation of *Tilletia*. If a spore of *T. tritici* germinates under water, the germ-tube grows until it reaches the air, and then only are the sporidia produced at the apex. The promycelium is thus shortest when grown in moist air; and when grown in water, of varying length according to the depth of the layer to be traversed (see Brefeld, p. 198). The agreement with the behaviour described for the promycelium of the Uredineæ is therefore exact. In *Ustilago*, on the other hand, the sporidia are freely formed while the promycelium is submerged.

It is curious that this exact relation, apparently so easily ascertainable, should in the Uredineæ require definitely stating; one can hardly believe that it has been overlooked by all the workers on teleutospore germination, but no suggestion of it could be found in botanical literature except the statement of De Bary (p. 281) "The simple tubes which may develop from the [teleuto] spores of Endophyllum when they are placed under water do not become promycelia, and are, as far at least as we at present know, incapable of further development." This would appear to show that De Bary recognized that in *Endophyllum* at least, air was necessary for the formation of the sporidia, but it remains an isolated statement made in relation to the question of the stages of complexity of development of the Uredineæ. Tulasne (p. 127) and De Bary (p. 350) recognized that teleutospores placed in water germinate with more difficulty than those in moist air, but neither makes any reference in this connection to sporidia formation.

As was mentioned above, germ-tubes produced in water continue to grow, usually in a more or less straight line (without showing any chemotactic attraction towards the surface of the drop), but in one case the apex of a long submerged tube had become divided into four cells (fig. 6), which bore some resemblance

to the sporidia-bearing cells; they had, however, rounded themselves off and begun to separate, and must probably be looked upon as chlamydospores. One of them had put out a small prolongation, either a short germ-tube or perhaps an abortive sterigma; the fate of these structures is unknown.

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DESCRIPTION OF FIGURES ON PLATE I.

Illustrating Mr. V. H. Blackman's Paper on Teleutospore Germination.

Figs. 4-6. *Phragmidium rubi*, Wint.

Fig. 4. A living Teleutospore germinating under water (×450).

Fig. 5. A Teleutospore germinated in moist air; from a fixed and stained preparation (×450).

Fig. 6. Apical portion of long germ-tube growing in water which has broken up into four chlamydospore-like bodies; from a fresh preparation (×450).

ON THE OCCURRENCE OF *TRISTICHA ALTERNIFOLIA*, TUL., IN EGYPT.

BY GULIELMA LISTER.

[WITH FIGS. 1-3 ON PLATE I.]

IN the early part of February, 1900, while passing in one of the native boats among the islands below the first cataract on the Nile, my attention was drawn to a brilliant crimson moss-like plant that was covering part of some of the rounded granite rocks projecting from the rushing water. On near approach, the plant was seen to be clothing the rocks for about a foot above water-level, and extending for a considerable depth below, covering altogether an area of about ten square yards; the upper part was dry and knotted into tufts of a drab or greenish colour, while where it was wet and fresh the colour was red. It seemed probable from its manner of growth that the plant belonged to the *Podostemaceæ*, and a fair quantity was scraped from the rocks, the swiftness of the current making the process not easy; search was made for flower or fruit without success.

On our return to England the plant was referred to Professor Warming, of Copenhagen, who identified it as being in all probability the var. *pulchella* Warmg. of *Tristicha alternifolia* Tul.; he has since published a description and figure of this gathering in the sixth of his Memoirs on the Podostemaceæ,[1] and mentions that this is the first record of the order from Egypt. As his full account is in the Danish language, I venture to give here a further description.

The Podostemaceæ are a family of, for the most part, inconspicuous plants, growing on rocks and stones in rivers and streams, and resembling mosses, seaweeds or lichens in their general appearance. They are submerged for the greater part of the year, and flowering takes place during the short time when the water is low and they are exposed to the air. An interesting feature of the group is the so-called "thallus," which either creeps and branches close over the surface of the rocks or sends up erect branches which may again give rise to leafy shoots; in some cases the branches are produced endogenously, and their extremities may or may not be provided with a root cap, or they may arise exogenously, or again, as Mr. Willis has shown, both modes of origin may occur

[1] Mém. de l'Acad. R. des Sci. et des lettres de Danemark, 6me Série, Sect. des Sciences, T. xi., No. 1, p. 37, 1901.

on the same thallus; so that there appears to be often no sharp division of the plant into stem and root. From the structure of the flower the order is considered by Professor Warming as probably most closely allied to Saxifragaceæ; it comprises about 120 species, which have been grouped under twenty-one genera. They are found in the tropical parts of Asia, Africa and America, and one genus extends into N. America.

The genus *Tristicha* contains, according to the researches of Professor Warming, but two species. *T. hypnoides* Spr. occurs in a great variety of forms in Central and South America, and South and Tropical Africa, including Abyssinia, Madagascar and Mauritius. *T. alternifolia* Tul., its near ally, has been recorded from Central and West Africa and Madagascar. They both have a moss-like habit, and the leaves are arranged along the leafy shoots in a more or less tristichous order: the small flowers are terminal on short branches, and possess a membranous three-lobed perianth, a single stamen, a three-celled ovary with free styles, and numerous ovules. *T. alternifolia* differs from its ally in having longer narrower leaves, less clearly tristichous in arrangement, the flowers often in pairs, and capsules on longer pedicels.

The Egyptian specimens consist of small pieces of the brown fleshy creeping thallus, from which arise slender leafy stems measuring half to three-quarters of an inch in length. The thallus is made up in part of smooth branching lobes that may be regarded as roots, although no root-cap is developed; the branches develope endogenously, and grow over and about one another, and were firmly attached to the rock by numerous clamp-like root hairs. The rest of the thallus consists of short flattened creeping stems with small scale-like leaves scattered over the sides and dorsal surface; from the sides of these short stems, in the axils of the leaves, the long slender stems arise.

The epidermis of the thallus is composed of small flattened rectangular cells, many of which contain plate-like siliceous bodies that are characteristic of the family. Beneath this, and forming the principal mass of the thallus, is a thick-walled parenchymatous tissue, without inter-cellular spaces, richly stored with starch granules; siliceous bodies occur here also, and are larger and stouter than those of the epidermis; they are rectangular or resemble short rods in shape, and show a grooved and pitted surface. They are well seen when sections of the thallus have been treated with a solution of chromic acid.

Each branch of the thallus is traversed by a vascular strand, the xylem lies on the ventral side, and is represented by a few long annular or spirally marked tracheides; dorsal to these are the long narrow sieve tubes with their companion cells. In older thalli these become obliterated. Professor Warming describes a well developed root-stele of the Podostemaceæ as being formed of two collateral bundles, with no alternation of xylem and phloem, which almost fuse together in the middle line to form a monarch system, the xylem occupying the ventral and the phloem the dorsal side. In this Egyptian specimen the double character of the vascular strand could not be detected. The long slender stems are either simple, or have one or more branches which originate as axillary buds: the vascular bundle is here a strand of long narrow cells that show no spiral or annular thickenings.

In each group of leafy shoots one shoot is often shorter and more procumbent than the others, while its leaves are more closely imbricated and distinctly arranged in the three rows characteristic of the genus *Tristicha*, one row being dorsal and of short leaves, the two lateral rows being of longer leaves. In the ascending stems the leaves are more irregularly scattered; the lower are rounded or oblong, but they gradually become longer as they ascend, and those forming the terminal tuft are narrowly linear and measure 3·5 mm. in length by 0·2 mm. in breadth. Each leaf has a midrib, formed of several layers of cells, extending more than half-way; the remainder of the leaf consists of a single layer of rectangular or long hexagonal cells containing chlorophyll whose green colour is masked by red colouring matter. Here and there, on either surface of the leaf, short cells are met with cut off obliquely from the distal extremity of the longer cells; they contain granular protoplasm and show a conspicuous nucleus. Siliceous bodies are often deposited in these cells, and when treated with chromic acid appear as strongly refracting H-, V- or Y-shaped objects with deeply crenulated outlines: they are also present in small tooth-like cells along the margins of the leaves, but the Egyptian specimen is singular, compared with other examples of *Tristicha alternifolia* in the scantiness of these siliceous deposits.

The winter of 1900 no doubt afforded very unusual conditions of exposure to a delicate plant like the *Tristicha*, for the Nile was lower than had been recorded for forty years. As a rule the river is lowest at the end of May; in June it begins to rise and attains its full height about the end of October, which at Assouan amounts to a rise of forty feet above the level in May. Thus at the

beginning of February, when the gathering was made, the plant was exposed some months earlier than usual, and this no doubt accounts for our having been fortunate enough to meet with so conspicuous a growth.

DESCRIPTION OF FIGURES ON PLATE I.

Illustrating MISS G. LISTER'S Paper on *Tristicha alternifolia*, Tul.

Fig. 1. Group of six leafy shoots and a bud arising from the margins of a broad creeping stem on which are scattered small scale-like leaves; one shoot has distinctly tristichous leaves; below are several broken roots; one to the right shows an old scar and from this a new root has grown out. × 6.

Fig. 2. Apex of leaf showing eleven siliceous bodies, seven on the upper, three on the lower surface, and one in a marginal cell: three short cells are drawn containing granular protoplasm and without siliceous bodies. × 170.

Fig. 3. Siliceous body from a leaf that has been treated with chromic acid. × 930.

ON THE IDENTITY OF *SPOROCARPON ORNATUM*, WILLIAMSON, AND *LAGENOSTOMA PHYSOIDES*, WILLIAMSON.

IN his 10th Memoir *On the Organisation of the Fossil Plants of the Coal-Measures*[1] the late Professor Williamson described and figured a transverse section of a small undetermined object from Halifax which he named provisionally *Sporocarpon ornatum*. His figure shows a circular cavity enclosed in a parenchymatous investment, the latter having an undulating peripheral boundary. Each of the nine or ten projections of the envelope bears "a cluster of very large thin-walled cells, most of which are prolonged radially.[2]" In his 13th Memoir[3] he figures a similar section from

[1] Phil. Trans. 1880, p. 510, and Pl. xviii., Fig. 39.

[2] loc. cit., p. 511.

[3] Phil. Trans. 1883, p. 469, and Pl. xxxi., Fig. 27.

Ashton-under-Lyne,[1] showing the existence of a canal in the centre of each of the projections or crenulations, whilst the peripheral clusters of large cells are wanting.

The object of the present note is to record the fact that *Sporocarpon ornatum* is nothing else than a transverse section of *Lagenostoma physoides*, a seed of which longitudinal sections had already been described and figured by Williamson in his 8th Memoir.[2] This identification is based on a comparison of the specimens in the Williamson Collection with others lately received from Mr. James Lomax, of Bolton. The agreement between the transverse and longitudinal sections is convincing in respect of structure, mode of preservation of the various layers, and dimensions. It is intended at some future time to describe the additional features that have been ascertained concerning the structure of this very interesting and little-known seed of the English Coal-Measures. In conclusion the writer would express his indebtedness to Miss Benson of the Royal Holloway College, and to Dr. D. H. Scott, F.R.S., who have kindly permitted him to examine preparations in their possession.

F. W. OLIVER.

[1] In the explanation of the figures, loc, cit., p. 474, this section is by an oversight named *Sporocarpon anomalum*.

[2] Phil. Trans. 1877, p. 241, and Figs. 77, 78 and 79.

PROFESSOR BOMMER ON LEPIDOCARPON.

ON the 18th of March last, my friend Professor Charles Bommer gave an account of the new genus *Lepidocarpon*, before the Belgian Geological Society.[1] Such a critical discussion of recent work is greatly to be welcomed, especially by the author whose work is discussed; it is a pleasure to me to find, in this instance, that the views of Professor Bommer, as regards the wider questions involved, are in essential agreement with my own. There are one or two points, however, where his interpretation does not seem to

[1] Le Genre Lepidocarpon, Scott; Bull. de la Soc. Belge de Géologie, t. xvi, 1902, pp. 132-137.

me to be entirely in accordance with the observed facts; these points I propose briefly to reconsider here.

Lepidocarpon, it will be remembered[1], is a Lycopodiaceous fructification of Carboniferous age, remarkable for the seed-like character assumed by the mature megasporangia.

This character depends chiefly on two facts:

1. That in each sporangium only a single megaspore came to maturity, forming the prothallus within it, and occupying, like an embryo-sac, almost the whole of the sporangial cavity.

2. That an envelope grew up from the sporophyll around the sporangium, completely enclosing it, except for a narrow crevice along the top. Further, all the evidence shows that the megaspore was retained permanently within the seed–like organ, which, like a true seed, was shed as a whole.

The chief point to be noticed concerns the nature of the envelope or integument. Professor Bommer says (p. 134); "Les sporanges . . . . . . sont protégés par les bords de la sporophylle qui, en se repliant audessus d'eux, leur constituent une enveloppe close et resistante," etc.

This interpretation of the integument as consisting of the infolded edges of the sporophyll is one which I have considered in my paper, and rejected, on grounds which Professor Bommer has not dealt with in his review. My reasons were these:

1. In the distal part of the sporophyll the lamina is clearly seen projecting laterally beyond the base of the integument, which cannot therefore be identical with it[2];

2 There is good evidence that the integument was closed at its proximal end (towards the axis) a condition which a mere infolding of the margins will obviously not account for.[3]

These important points appear to have escaped Professor Bommer's attention, for he merely refers to the presence of

[1] Scott, Structure and Affinities of Fossil Plants from Palaeozoic Rocks; IV. The seed-like Fructification of Lepidocarpon. Phil. Trans. Roy. Soc. B. vol., 194, 1901. See also NEW PHYTOLOGIST, February 1902, for a review by F. W. O.

[2] Scott, l. c., p. 306, Pl. 41, Fig. 13.

[3] l. c., p. 308, Pl. 43, Fig. 24.

lateral furrows in the sporophyll of *Lepidocarpon Lomaxi*, a fact on which I have laid no stress, as it has no evident bearing on the question as to the nature of the integument.

The author considers the species *L. Wildianum* especially favourable to his interpretation, but I have not found any essential difference between the two species; in *L. Wildianum* also there is evidence for the presence of a laminar margin distinct from the integument.[1] On a consideration of all the facts, it seems clear that the integument in the genus *Lepidocarpon* was a new formation, not represented in the young sporophylls or in those of ordinary Lepidostrobi. Neither is the velum of *Isoëtes* formed by the infolded margins of the sporophyll, as Professor Bommer, no doubt by an oversight, states (p. 135); his own figure shows that this is not the case.[2] The velum of *Isoëtes* springs partly from the saddle at the distal end of the sporangium, partly from the upper surface of the sporophyll-base, but not from its margins; like the integument of *Lepidocarpon* it is a new formation—an indusium. I agree with Professor Bommer that the integument of a seed is also a sort of indusium (p. 136).

The statement that in *Lepidocarpon* the sporangium is protected by the whole of the sporophyll is true, but with the reservation that this protection is only carried out with the help of a new organ, the integument, specially adapted to this function. That the sporophyll as a whole takes part in the formation of the seed-like organ is a real point of difference from a typical seed, as I had already stated.[3]

In conclusion our author remarks that there are two facts which materially reduce the morphological importance of the integument of the megasporangia in *Lepidocarpon* (p. 136). One of these facts is the presence of a similar protective envelope around the microsporangia. On this point I have nothing to add to what is said in my paper (p. 322). An envelope originally common to both kinds of sporangia may well have been retained and further developed on the female side only, where its functions would obviously be more important. In our fossil there is already a considerable difference between the integuments of the two organs, for that of the microsporangium forms only a very partial investment.[4]

[1] l. c., p. 316, Pl. 42, Fig. 18.

[2] See also Campbell, Mosses and Ferns, Fig. 144, B.

[3] l. c., p. 321.

[4] l. c., p. 313.

Professor Bommer's second point is the fact that so many of the megasporangia are without any integument. I have suggested that these specimens may represent the young stage of the organ in an arrested condition, to which our author objects that the suggested arrest of development only affects the external envelope, the megaspore, which is the essential part, being fully formed. Since my paper was published I have observed a non-integumented sporangium in which the megaspore already contains a prothallus,[1] a fact which no doubt adds force to Professor Bommer's criticism. Still, I can see no other explanation of the facts than that, from some cause or other (possibly the absence of pollination), certain sporangia were arrested in their development before the integument was formed. That among equally mature organs some should be with and others without such an important appendage, seems highly improbable, though perhaps a remote analogy might be found in the inconstancy of development of the indusium in some Ferns.

Although I am not able wholly to accept Professor Bommer's interpretation of the structure of *Lepidocarpon*, we are in substantial agreement in our views of the general significance of the type of fructification which it exhibits, and in our estimate of its biological importance. In his concluding paragraph Professor Bommer sums up the question in some admirable remarks with which I am entirely in accord.

" En résumé, *Lepidocarpon* nous offre l'exemple d' un Lycopodinée trés évoluée par l'accentuation d'une série de dispositions spéciales, réalisées déjà isolément ou à un moindre degré chez d'autres Ptéridophytes, Les charactéres particuliers d'adaptation de son appareil de reproduction offrent, fonctionnellement, un parallélisme remarquable avec ce qui existe chez les Phanérogames."

D. H. SCOTT.

[1] This section is in the Collection of Fossil Slides belonging to the Botanical Department of University College, London.

SOME RECENT OBSERVATIONS ON MYCORHIZA.

SOME interesting additions to our knowledge of that striking, and, as is now known (see New Phytologist, Vol. I., p. 83, April, 1902), extraordinarily wide-spread phenomenon, "Mycorhiza," have recently been made by the Japanese observer Shibata.

His work was chiefly done on infected roots of species of *Podocarpus*, on *Psilotum triquetrum*, and also on *Alnus* and *Myrica*. *Podocarpus* is of special interest in this connexion, since, according to the experiments of Nobbe and Hiltner, infected plants of this genus are able to assimilate free nitrogen. The cells of the root-tubercles (produced by the modification of secondary roots) soon become filled with masses of strongly-developed mycelium in which cross-walls are absent. The contents of the cells of the host early begin to react very markedly to the presence of the fungal hyphae; not only does the cytoplasm become increased in amount, but the nucleus also grows in size and has more stainable contents, while at the same time it becomes irregular in form. It then elongates and divides into two by simple direct division, a process which continues till as many as eight nuclei are found in a single cell. They are irregular and lobed in shape, and appear as compact masses of chromatin. While these changes are taking place in the nuclei the fungus mycelium begins to shew signs of disorganisation; the contents of the hyphae become gradually lost, the thin walls at first collapse, and later, in spite of the fact that they consist largely of chitin, almost completely dissolved, so that finally scarcely a trace of the attacking fungus is to be found in the cells of the host.

The behaviour of the nuclei and the progressive disorganisation of the fungal hyphae strongly suggest that a ferment or ferments have been secreted by the host-cells, and that this has led to the almost complete solution of the mycelium. Shibata has in fact actually demonstrated the existence of a proteolytic ferment in the infected tubercles of *Podocarpus*, since an extract of these when slightly acidified was found to dissolve fibrin, while an extract of similar uninfected tubercles had no such effect. It was further observed that the nuclei of the host-cells, after abosrption of the fungus, returned to their normal state, and were capable of dividing by the normal karyokinetic method, exhibiting the typical number of chromosomes.

Similar cytological observations were made on the cells of the

roots of *Psilotum*, which had been infected with mycorhiza. Here the nuclei of the host-cells increased enormously in size and contents, while the contents of the hyphae were completely absorbed, the chitinous walls, however, remaining behind as an undigested clump in the cell.

In the case of the root-tubercles of *Alnus*, to which Nobbe and Hiltner also ascribed the power of fixing free nitrogen, a proteolytic ferment was again demonstrated, though the symbiont is here not a true fungus, but like that of the well-known root-tubercles of Leguminosae, a bacterium-like organism.

In *Myrica* the fungus of the tubercle is confined to a definite ring consisting of one to three layers of parenchyma, and there is progressive infection of the new tissues formed at the apex of the tubercle. The radiating arrangement of the hyphal branches of the fungus, together with the club-shaped swellings of their ends, point to a relationship with the genus *Actinomyces*. Here in fact we seem to have a case of vegetable "actinomycosis."

Altogether these observations extend our knowledge of the relation of host and parasite in a most interesting manner. They extend the conclusion already arrived at in the case of Leguminous tubercles and of the saprophytic prothalli of Lycopods and Ophioglossaceae (see NEW PHYTOLOGIST, April, 1902, p. 87) of the complete mastery of the plant over its symbiont. The relations of nutrition are not yet, however, by any means clear. We do not know how the plant is enabled to fix free nitrogen. The supply of any sort of food to the host from the exterior by the aid of the fungus would seem to be difficult, since the external connexions of the latter are very slight.

V. H. B.

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RECENT DISCOVERIES OF CAOUTCHOUC IN PLANTS,

BY F. E. FRITSCH, B.SC., PH. D.

SINCE Radlkofer[1] showed that the laticiferous elements of *Parameria vulneraria* contain threads of semi-solid caoutchouc—readily observed, when any part of the plant is broken into two, and the halves are carefully drawn asunder—similar occurrences have been recorded in plants belonging to diverse natural orders. Thus *Eucommia ulmoides* was found to possess such threads[2] throughout all parts of the plant, whilst Radlkofer in a later paper[3] mentions their presence in *Wimmeria cyclocarpa* and in *Plagiopteron* (a genus at that time included in the heteropetalous Tiliaceae); he further adds, that similar threads have been observed by Solereder to occur in *Salacia micrantha* Peyr., as well as in three Hippocrateaceous stems belonging to Schenck's collection of tropical lianes. A detailed investigation of the Hippocrateaceae, undertaken by the writer some little time back,[4] led to the recognition of the fact that these threads occur in a considerable number of species. Finally Col[5] has quite recently shown them to be present in the genus *Evonymus*, although here, as will be more fully explained below, they are not evident except in plants of some years' growth. These recent observations tend to show that the elastic threads of caoutchouc are of far more frequent occurrence than was at first supposed. This interesting subject seems to me to have been little noticed in this country and I therefore propose to devote the following pages to a brief description of the essential features.

[1] Radlkofer, Ueber eine Daphnoidee, etc. Sitzungsber. d. mathem-phys. Klasse d. k. k. Akad. d. Wissensch, Munich, Vol. XIV., 1884. p. 515.

[2] Cp. Hooker, Icones Plantarum, 3rd series, Vol. XX., 1890; and Weiss in Trans. Linn. Soc. Vol. III., 1892. Part 7. p. 243.

[3] Botanical Gazette. Vol. XVIII., 1893, p. 199-200.

[4] Cp. Bot. Centralblatt. 1901. Beihefte Vol. XI. Part 5. Only dried material was available.

[5] Comptes Rendus des Séances de l'Acad. d. Sciences, Paris, June 1901.

If any portion of a plant of *Plagiopteron fragrans*, Griff, *Salacia micrantha*, Peyr, or of a species of *Wimmeria* be carefully broken into two, it will be remarked, that the two fragments still hang together by means of a number of thin white threads. If slowly drawn apart, it will be found that the two fragments can be separated some little distance from one another before the connecting threads snap; and the elasticity of the latter is so great, that on relaxing the tension the two pieces again resume a position of close proximity. This curious feature has naturally not been absolutely unobserved by earlier botanists, although incorrectly interpreted. Thus Petit-Thouars[1] in 1806 figures these threads in the fruit-wall of *Salacia Calypso*, DC, a plant, abounding in them; whilst De Candolle[2] in 1824 remarks: "*Hippocrateae ovatae* spermodermium et cotyledones intus singulari modo filis innumeris tracheiformibus stuposi! quod etiam in *Calypsois* suae pericarpio vidit cl. Petit-Thouars." Further Griffith[3] in his original description of *Plagiopteron fragrans* remarks, that the plant "abounds with spiral vessels."

The material, constituting these threads, differs from ordinary latex in being in a semi-solid state; it is insoluble in alcohol, whereas it is more or less completely dissolved by ether, benzol or chloroform. In polarised light it is strongly doubly refractive, this property being lost temporarily or permanently when heat is applied. The threads have the capacity of taking up certain stains very readily, although the different genera and species vary considerably in this respect. On evaporation of the benzol-solution, a thin greyish-white elastic film remains, which burns with the smell characteristic of burning rubber. These characters point to the threads consisting of a kind of caoutchouc; according to the French investigators it is more of the nature of gutta-percha.[4] With regard to the quantity of caoutchouc present it is noteworthy that the bark of *Eucommia* has yielded as much as 5.7 °/₀,[5] whilst Col finds that 50 grm. of the bark of *Evonymus japonicus* yield 5 grm. Many species of Hippocrateaceae must be as rich, if not even richer than this.

The histological elements, in which this caoutchouc is contained, are of the nature of laticiferous cells (or cœnocytes ?). In a number

[1] Histoire des Végétaux D'Afrique. 1st Part, p. 20.

[2] Prodromus. I., p. 569, foot-note.

[3] Calcutta Journal of Natural History. Vol. IV., p. 246.

[4] cp. Barthelat in Journal de Botanique. Vol. XIV., 1900. nr. 2; and Col, loc. cit.

[5] Bulletin of Miscellaneous Information, Kew. September 1891.

of species of Hippocrateaceae and in *Plagiopteron* these cells attain so great a length, that I have rarely observed a termination in those which traverse the stem; nor do transverse partitions occur in their course. In the case of *Hippocratea ovata* Lam. it has been possible to show that these caoutchouc-cells are present in the embryo in the seed, where they occur very abundantly in the cotyledons. Hence they are comparable to the latex-elements of Moraceae, Apocynaceae, etc.; a similar eariy development is probable for the other species.[1]

They are present in both primary and secondary phloem of the stem, as well as in the primary cortex; in *Plagiopteron* alone they are found in the pith. While very common in phloem and cortex of the petiole, in the leaf they are restricted to the under-side of the veins, where they usually replace part or all of the sclerenchyma, accompanying the vascular bundle. Here however branching, which is very rare in other portions of the plant, is of common occurrence in some species. The branches originate from the laticiferous elements, accompanying the vascular bundles, and ramify freely in the spongy tissue; only rarely do they pass into the palisade-parenchyma. Caoutchouc-cells occur throughout all parts of the flower, penetrating alike into sepals, petals, stamens and style.

Laticiferous elements of this type, extending throughout all the organs of the plant, are found in all species of *Wimmeria*, in *Plagiopteron* and in a number of the Hippocrateaceae. Other members of this latter order however have caoutchouc-cells of a different type, also occuring in *Evonymus* and other genera of the Celastraceae proper.[1] In these cases no laticiferous elements are to he found in young branches, although those of some years' growth are often very rich in them; thus a stem of *Salacia Roxburghii*, measuring about 1 cm. across, is devoid of these structures, whereas one of about 2½ cm. diameter was found to contain them very abundantly in the secondary portion of the rind Apparently the stage at which they begin to appear, is arrived at earlier in the growth of some species, than in that of others, so that it is quite possible that the list of caoutchouc-containing species will be considerably increased when opportunities for the examination of thicker stems are afforded. Some species of Hippocrateaceae however certainly never possess caoutchouc,[2] since it is wanting in

[1] It is no easy matter to obtain the fruits of species of Hippocrateaceae, so that an investigation of the seed has only rarely been possible. As for *Plagiopteron*, although I have examined a number of fruits, they were always devoid of seeds, the ovules having apparently aborted

a number of Schenck's lianes. It remains to be seen whether such caoutchouc-cells ars equallly abundaut in thick stems, belonging to the various genera of Celastraceae proper.

Their late appearance is not the only striking point about these elements. They are absolutely restricted to the axis of the plant (*i.e.* stem and root) and are wanting in petiole, leaf and flower. In the stem they occur only in the secondary portions of the cortex, none of the species, as yet investigated, has shown them in the pith. Those belonging to the secondary phloem, are characterised by their relatively straight course and their terminations are not rarely met with in longitudinal sections; these terminations are however difficult to find in the caoutchouc-cells of the phelloderm[3] since these usually have a very tortuous course. They appear to wind their way in and out between the cells, so that a longitudinal section frequently shows one of them cut transversely. This is at all events the case in *Hippocratea Grahami* and *Salacia Roxburghii;* in *Evonymus japonicus* they are apparently confined to the secondary bast.

Col remarks that the caoutchouc-cells appear in the root of *E. japonicus* before secondary tissues arise. In certain species they are common in the primary phloem of the rootlets, the laticiferous cells extending to the very tips of these organs. Thick roots contain even more caoutchouc than do stems of the same diameter.

The above-mentioned terminations are frequently observed in longitudinal sections; in *Evonymus* the caoutchouc-cells are drawn out to a fine point, in the species of Hippocrateaceae investigated the ends are blunt and broad. According to Col these cells in *Evonymus japonicus* vary in length from ·5 mm to 2 mm. I have as yet been unable to determine their length in Hippocrateaceae, but, as far as my observations go, I should think that they are often longer than in *Evonymus.*

With regard to the mode of development of these laticiferous elements nothing definite is at present known; but owing to their general appearance and their determinate length a mode of development similar to that of the caoutchouc-cells of *Eucommia*, as described by Weiss, seems probable, that is to say it seems likely

[1] M. Col has most kindly informed me by letter of their occurrence in *Maytenus Vitis Idaea.*

[2] It should however be remarked that all species of Hippocrateaceae contain more or less numerous small lumps of a substance, behaving physically and chemically like caoutchouc in the cells of the mesophyll.

[3] There is apparently a considerable development of phelloderm in the Hippocrateaceae.

that they may arise by differentiation and stretching of ordinary parenchymatous cells, which in their later elongation push their way in and out between the surrounding cells. The tortuous course of the caoutcbouc elements in the secondary cortex of the above-mentioned Hippocrateaceae seems very suggestive of such an origin.

It is perhaps a little premature to talk of the phylogenetic importance of this type of laticiferous element; but so much may be pointed out, that the occurrence of unbranched latex-cells (sacs, confined to the axis and of determinate length) and of branched laticiferous elements (occurring throughout the plant and attaining a great length), in species of the same genus tends to support the views, expressed by Weiss.[1] This investigator looks upon *Eucommia* as possessing "a primitive, though not the most primitive form of a latex-cell." He further remarks: "The caoutchouc-containing cells of *Eucommia* are unbranched and still contain only one nucleus, but it is easy to conceive that a division of this nucleus into several younger nuclei, a division which might become necessary by the dimensions of the cells, would enable the cell under certain conditions to branch out in other directions, as it has become normal for the latex-cells of the Euphorbiaceae." Should a more detailed investigation show that the unbranched latex-cells of Hippocrateaceae contain only one nucleus whereas the branched elements are multinucleate,[2] the phylogenetic connection suggested by Weiss, will be fully established. In their late appearance and their restriction to the axis the unbranched caoutchouc-cells of the Hippocrateaceae and of *Evonymus* seem to be more primitive than those of *Eucommia*.

It might be imagined that the laticiferous cells (sacs), found in *Evonymus*, *etc.*, gradually began to make their appearance at an earlier stage in the development of the plant and also to extend into the lateral appendages; in this way the type of latex-cell, found in *Eucommia*, may have originated. Multiplication of the nuclei in a laticiferous element of this type would tend to produce an increase in size of the element in question and ultimately lead to a certain amount of branching taking place. Under these circumstances the number of the individual latex-cells could be considerably diminished. We thus reach the type of laticiferous element, occurring in many Euphorbiaceae and in the Apocynaceae, Urticaceae, etc. This evolution of the branched from the unbranched type has, as is

[1] loc. cit. p. 251, 252.

[2] Attempts to stain the nuclei have as yet proved unsuccessful.

pointed out above, probably taken place in the Hippocrateaceae with (as far as our present knowledge goes) the omission of the type found in *Eucommia.*

With regard to the possible function pertaining to these caoutchouc-containing cells, which, as we have seen, occur so abundantly in certain groups, nothing can be said until an examintion of a number of living plants has been undertaken. The semi-solid condition of the contents does not admit of their being regarded as channels for the conveyance of food-material. Possibly they may be of use in sealing up wounds after the manner of the resin-ducts of Conifers.

ON SAPROPHYTISM AND MYCORHIZA IN HEPATICAE.

By F. Cavers, Yorkshire College, Leeds.

THE occurrence of fungal hyphae in the tissues of Hepaticae appears to have been first described in detail by Leitgeb[1], who observed that the young sporogonia of *Ptilidium ciliare* were frequently infested by the mycelium of a fungus. Leitgeb found that these sporogonia showed a different mode of segmentation from that usually observed in the Jungermanniaceae, and believed that this might be due to the presence of the fungus. In examining a considerable number of Hepaticae, the writer has several times observed sporogonia around and within which fungal hyphae were growing. The life-history of the fungus was carefully followed in the species of which living material was available, namely, *Lophocolea bidentata, Cephalozia bicuspidata, Plagiochila asplenioides,* and *Radula complanata.* The fungus-infested sporogonia are, as a rule, imperfectly developed and remain enclosed within the calyptra. The fungal hyphae usually enter the fertilised archegonium from above, growing down the neck-canal, but in some cases they pierce the venter and thus reach the young sporogonium directly. The infected sporogonia are, as a rule, imperfectly developed, showing a few irregular divisions and remaining abortive. In cases where devolopment has proceeded as far as the differentiation of the capsule, the cavity of the latter is generally filled with a mass of interlacing hyphae, in which are embedded numerous small spherical bodies, which arise by abstriction from the hyphae and are therefore to be regarded as the conidia of the fungus.

[1] Leitgeb, Untersuchungen über die Lebermoose, Heft 2, p. 58; Taf. 3, fig. 26.

It has long been known that in the Bog-mosses (Sphagnaceae) the capsule occasionally contains numerous small spores which to a greater or less extent replace the ordinary spores of the moss. To these small spores Schimper[1] gave the name "microspores," his interpretation of these bodies, which has been copied into nearly all the text-books, being that they arise by continued division of the spore-mother-cells. According to Warnstorf,[2] the occurrence of these "microspores" is observed more frequently in the monoecious than in the dioecious species of *Sphagnum*, and he suggested that this might be a case of heterospory, analogous to that observed in certain Pteridophyta and all Spermaphyta, the "microspores" giving rise to the male plants, whilst the ordinary large spores produced the female plants. However, the observations of Nawaschin[3] showed that the "microspores" are produced by a parasitic fungus *(Tilletia Sphagni)*, the mycelium of which ramifies through the sporogenous tissue of the capsule.

Warnstorf's statement that "microspores" were also observed by him in *Pallavicinia Lyellii* led the writer to examine this liverwort, a few young capsules of which were found in Husnot's "Hepaticae Galliae" (No. 167). The investigation of this material showed the presence of a fungus, and in some cases "microspores" were seen arising by abstriction from the fungal hyphae, so that here, as in the liverworts already referred to, these bodies are simply the conidia of a fungus. Fungal hyphae and spores were also in young capsules of *Pallavicinia hibernica*, material of which kindly sent by Mr. W. H. Pearson, of Manchester.

It would therefore appear that in those cases where a fungus-body has been found to inhabit the sporogonium in Bryophyta, the relation between the fungus and the host-plant is simply that of parasitism.

In certain mosses, as shown by the investigations of Haberlandt[4] and of Brizi,[5] the rhizoids penetrate the decaying vegetable tissue

[1] Schimper, Versuch einer Entwickelungsgeschichte der Torfmoose, 1858, p. 54.

[2] Warnstorf, Zur Frage über die Bedeutung der bei Moosen vorkommenden zweierlei Sporen. Verhandl. d. botan. Vereins d. Prov. Brandenburg, 1886; Revue bryologique, 1887, p. 15.

[3] Nawaschin, Ueber die Brandkrankheit der Torfmoose. Bulletin de l'Academie des Sci. de St.-Petersbourg. tome 35, 1892, p. 531.

[4] Haberlandt, Beitrage zur Anatomie und Physiologie der Laubmoose. Jahrb. für wissensch. Botanik, Band 17, 1886, p. 476.

[5] Brizi, Contributo allo studio morfologico, biologico, e sistematico delle Muscinee. Annuario del R. Ist. Bot. di Roma, vol. 6, 1897.

which forms the substratum, so that the moss-plant assumes a more or less saprophytic mode of life. A precisely similar adaptation has been found by the writer to exist in certain Hepaticae. Thus in *Lophocolea bidentata*, which frequently occurs on decaying wood, the gametophyte appears to be entirely free from fungal hyphae, but the rhizoids, which are borne in tufts at the bases of the amphigastria, penetrate the substratum, their ends becoming profusely branched, like the haustoria of many Fungi. In many exotic Lejeuneae and Frullaniae which grow on the stems and leaves of living trees, the rhizoids show a similar haustorium-like penetration of the substratum, and it is highly probable that they serve not only for attachment but also for the absorption of organic food-materials. In several specimens of these epiphytic liverworts (kindly presented to the writer by Mr. M. B. Slater, of Malton), the plants were found growing over lichens, into which the rhizoids had become inserted, undergoing repeated branching and becoming interwoven with the lichen-tissue in a complicated manner. Moreover, the parts of the liverwort which had thus become intimately connected with the lichen showed a more luxuriant growth than those that came into direct contact with the stems or leaves on which the liverwort and lichen were together growing as epiphytes; the leaves were larger, and in the case of Frullanias the increase in size of the water-pitchers ("lobules" or "auricles") was frequently very marked.

Fungal hyphae have been observed in the tissues of the gametophyte in a considerable number of Hepaticae, both thalloid and foliose, and in some cases there can be no doubt that the association of the fungus with the liverwort is of a symbiotic nature.

In 1879 Kny,[1] in describing the peculiar regeneration-process which is frequently observed in the rhizoids of *Lunularia* and *Marchantia*, namely, the development of secondary or even tertiary rhizoids within the primary rhizoids, states that the latter are sometimes traversed by branched but sterile fungal hyphae. The writer has found that when these liverworts are growing in ordinary soil, the fungal hyphae may penetrate the rhizoids, growing upwards as delicate filaments which show cross-walls at rather long intervals and occasionally become branched, but not reaching the compact tissue of the thallus. On examining plants that had been growing on rich humus, however, it was found that not only did the plain

[1] Kny und Bottger, Ueber eigenthumliche Durchwachsungen an den Wurzelhaaren zweier Marchantiaceen. Verhandl. d. botan. Vereins d. Prov. Brandenburg, 1879, p. 2 of separate.

rhizoids penetrate the tissue of the substratum (chiefly decaying leaves), but that both the plain and the tuberculate rhizoids were traversed by numerous hyphae which extended into the compact ventral tissue of the thallus, passing through the cell-walls and becoming frequently branched. The hyphae are confined to the lowest layers of the thallus, and the cells containing them appear in sections as a fairly well defined zone. In *Fegatella* (*Conocephalus*) *conica*, the fungal hyphae are sometimes very abundant, especially when the plants are growing in decaying organic matter. The writer has collected this liverwort on the sides of foul sewer-like streams issuing from tanneries and other works, where the plants grow luxuriantly in large patches on the slimy substratum and form practically the sole vegetation. In such plants, the fungal hyphae occupy nearly the whole of the compact tissue underlying the air-chambers. The hyphae frequently bear small conidium-like bodies and also large swollen vesicles filled with dense granular protoplasm. These vesicles may be either terminal or intercalary, and in the latter case are often aggregated in chains. Some of the vesicles are thin-walled, but many of them have thickened, highly refractive walls, and may be regarded as chlamydospores. The fungus-bearing plants are larger and thicker than those which are free from fungal hyphae, and there can be little doubt that we have here a definite symbiosis, the fungus forming a mycorhiza by means of which the life of the *Fegatella*-plant becomes to a large extent saprophytic. As shown by Beauverie,[1] who has briefly described the fungus inhabiting the thallus of *Fegatella*, the conidia and chlamydospores which are borne on the hyphae, both within the tissues of the thallus and in cultures, agree closely with those of *Fusarium*.

It may be noted that according to Czapek,[2] the tissues of *Fegatella*, *Marchantia*, and *Lunularia*, besides other Hepaticae, contain the antiseptic substance which he terms "sphagnol" on account of its abundance in the Bog-mosses. This substance was shown by Czapek to exist in combination with the cellulose of the cell-walls, and to exert an inhibitory influence on the growth of bacteria and moulds. This suggests the view that in the case of the Fusarium-like fungus the sphagnol may serve to regulate the growth of the fungus-body and to prevent symbiosis from passing into parasitism.

1 Beauverie, Étude d'une Hepatique à thalle habité par un champignon filamenteux. Comptes rendus de l'Acad. des Sci. de Paris, 1902, p. 616.

2 Czapek, Zur Chemie der Zellmemberanen bei den Laub. und Lebermoosen. Flora, Band 86, 1889, p. 361.

In September, 1902, the writer received from Mr. G. Webster, of York, a large supply of living specimens of a New Zealand liverwort, *Monoclea Forsteri*, which had been cultivated in a greenhouse. This plant has a broad creeping thallus, showing irregular dichotomous branching. In general habit the thallus resembles that of *Pellia*, but is broader and thicker. In every plant examined, vertical sections of the thallus showed a sharply defined mycorhizal zone, consisting of from two to four layers of cells densely filled with branching fungal hyphae. This zone is confined to the thicker median portion of the thallus and extends to within a short distance of the growing-point. In longitudinal sections of the thallus, the progress of the hyphae through the tissues can be followed step by step. As the hyphae pierce the cell-wall and branch out in the cell-cavity, the nucleus of the infected cell grows in size and often becomes enveloped by a tuft of short hyphal branches. All the cells of the thallus (excepting those which form rhizoids and certain scattered cells containing large oil-bodies) contain chloroplasts, and in some cases the latter become, like the nucleus, surrounded by tufts of short hyphae, in a manner strongly suggestive of the formation of a lichen. On some of the hyphae there are formed large spherical vesicles, many of which have thickened walls, as in *Fegatella*.

Golenkin[1] has recently shown that an endotrophic mycorhiza exists in *Marchantia palmata*, *M. paleacea*, *Preissia commutata*, *Targionia hypophylla*, and *Plagiochasma elongatum*, in addition to *Fegatella conica*. He states that in all cases the fungal hyphae are confined to the compact ventral tissue, and that the infected cells, though they retain their nuclei and protoplasm, never contain starch or chlorophyll. Golenkin compares the fungus with that found in the roots of *Neottia* and the prothallia of *Lycopodium*, and suggests that the function of the mycorhiza in the Marchantiaceae investigated by him is that of storing water and enabling the plant to resist drought. Against this view, however, it may be pointed out that (1) *Fegatella* and *Monoclea*, the forms which have been specially examined by the present writer and which have an exceptionally well developed mycorhiza, are typically hygrophilous plants, living on stones in streams and apparently not exposed in nature to the risk of becoming dried up; (2) in the case of *Fegatella* the storage of water is well provided for by the highly developed mucilage-organs, strings of large mucilage-containing cells which traverse the midrib, in addition to numerous scattered mucilage

[1] Golenkin, Die Mycorhiza-ähnlichen Bildungen der Marchantiaceen, Flora, Band 90, 1902, p 209.

sacs occurring in the compact tissue of the thallus and the sexual receptacles.

The presence of a symbiotic fungus has also been observed in several of the foliose Jungermanniaceae, and it is probable that here, as in the thalloid Hepaticae, further research will result in the recording of additional examples of this phenomenon. The occurrence of fungal hyphae in the rhizoids has been described by Janse[1] for *Zoopsis* and by Nemec[2] for *Kantia trichomanis*, *Lepidozia reptans*, and *Lophozia bicrenata*. To these species the writer can add the following, of which living material has been examined: *Cephalozia bicuspidata*, *Scapania nemorosa*, *Diplophyllum albicans*, *Plagiochila asplenioides*, *Bazzania trilobata*, and *Porella platyphylla*. The presence of the fungus appears to be correlated with the habitat of the plant. When the substratum consists of rich humus, fungal hyphae are nearly always to be found, even when they are absent from plants of the same species growing on ordinary soil or on stones. In some cases the swollen free end of the rhizoid is filled by a mass of branched and interwoven hyphae. As a rule, from two to six hyphae pass straight up the rhizoid, sometimes showing ladder-like fusions. At the upper end of the rhizoid, the hyphae become repeatedly branched, giving rise to a parenchyma-like mass of cells, which frequently send short finger-like processes through the cell-walls into the overlying tissue of the stem. As observed by Nemec in *Kantia*, the cells into which these processes project retain their living contents, whilst the nucleus of each cell comes to lie on the lower wall, in close contact with the fungus. From Nemec's observations on *Kantia*, it would appear that in this case the fungus is an Ascomycete (*Mollisia Jungermanniae*), which frequently grows on the liverwort, bearing little bluish-green apothecia and covering the plant with a web-like mycelium. The hyphae of this mycelium here and there penetrate the cells of the leaves and stems, and these infected cells soon lose their protoplasm and become discoloured.

It is, therefore, probable that in at least some of the cases in which fungal hyphae occur in the tissues of the liverwort-gametophyte, the hyphae belong to a fungus which may either grow as a parasite on the host-plant, or the latter may, as it were, gain the upper hand and cause the fungus to enter into a mutually beneficial partnership, forming a mycorhiza by means of which a more or less less saprophytic mode of life is established.

[1] Janse, Les Endophytes radicaux de quelques plantes javanaises. Annales du jardin botanique de Buitenzorg, vol. 14, 1897.

[1] Nemec, Die Mykorhiza einiger Lebermoose. Berichte der deutsch. botan. Gesellsch., Band 17, 1899, p. 311.

AFRICAN PARK-LANDS.

[Plate II.]

THE most fundamental classification of the different types of vegetation covering the earth's surface is that into Forest, grass-covered Steppe, and Desert. In his great work on Plant-geography[1] Schimper ably summarises the climatic conditions which govern the occurrence of one or other of these great "formations" over any tract of country. He comes to the conclusion that the main conditions under which Forest occurs are a comparatively warm vegetation period, a constant supply of water in the lower strata of soil reached by the roots of the trees, and a comparatively damp and still atmosphere. Grass-covered Steppes, on the other hand, demand for their existence frequent, if only slight, rainfall so that the surface of the earth is kept moist during the period of active growth, and a moderate equable temperature. In a general way, and apart from special conditions, the existence of one or other of these types of climate will determine the victory of one or other of these types of vegetation.

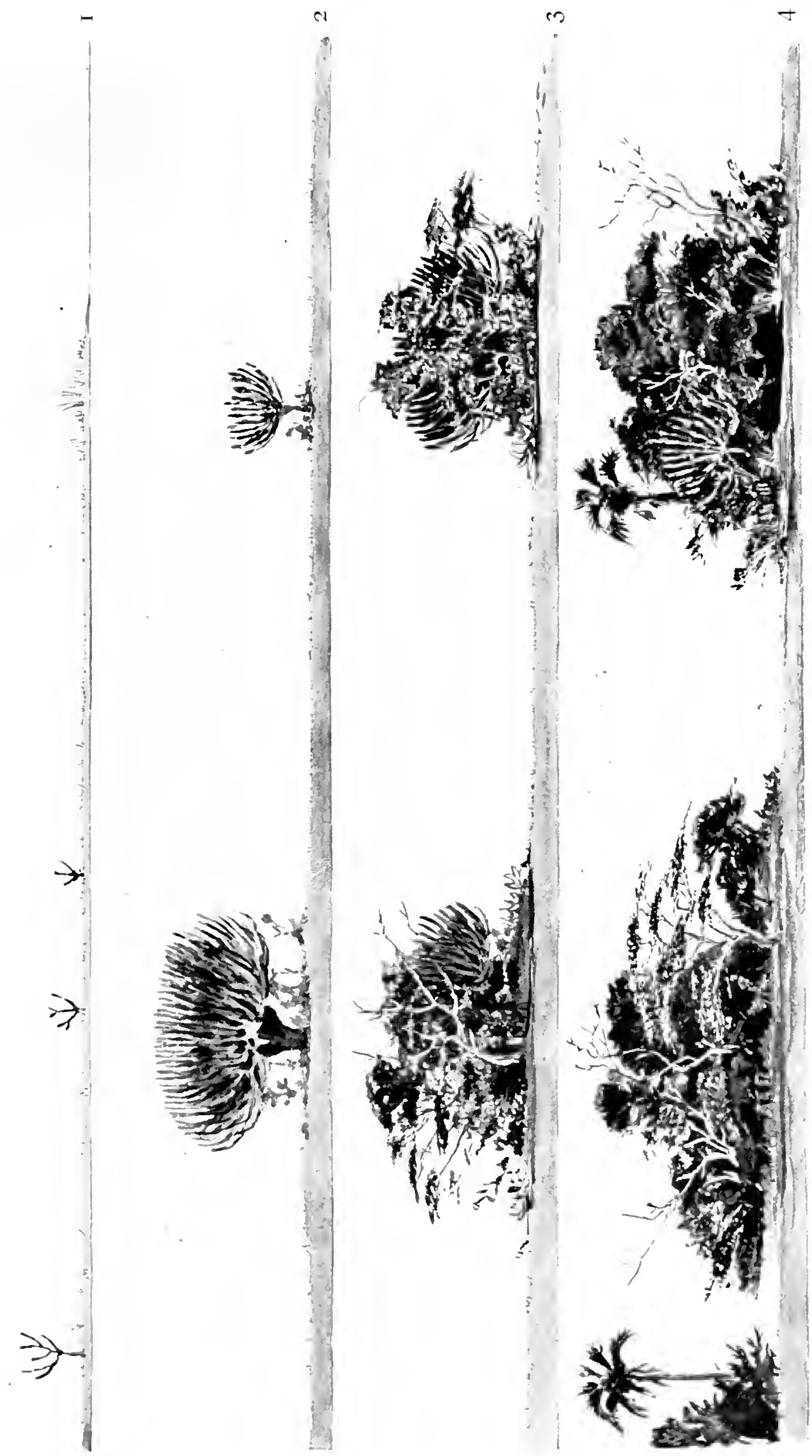
An intermediate type of vegetation, the Savannah or Park-Land in which grass-covered plains are dotted here and there with single trees or clumps of trees and shrubs, is however, characteristic of enormous stretches of country in the tropics, particularly in South America and in Central Africa, and this, according to Schimper and others, owes its existence to the prevalence of an intermediate type of climate, so that the balance is held, as it were, between the grass-formation and the forest-formation, and neither can gain the predominance. Schimper supports this theory by statistical data of rainfall, etc., and concludes that when there is a mean annual rainfall of more than 72 inches, typical forest occurs, while with a rainfall of 36 to 60 inches, we have a struggle between the grass-formation and the xerophilious forest.

Mr. J. E. S. Moore, however, in his recent fascinating volume[2] containing the scientific results of the two Tanganyika Expeditions, has thrown quite a new light on one aspect of this general question, and offers a convincing solution of the problem of how the Park-Lands, observed by him extending over great tracts of country between the Zambesi and the Albert Nyanza, have originated.

Stated in general terms Mr. Moore's view is that park-

[1] A. F. W. Schimper: Pflanzengeographie, 1898, pp. 176-190.

[2] The Tanganyika Problem, by J. E. S. Moore, London. Hurst and Blackett, 1903.



1. Albert Nyanza plains with straggling grass and Euphorbia seedlings.
2. Euphorbia casting shadow in which other plants spring up.
3. Clumps of trees and bushes which have established themselves round Euphorbia trees.
4. Typical Park-land passing to Forest. Euphorbia choked.

AFRICAN PARK LANDS.

TO FACE PAGE 38.

Reproduced from "The Tanganyika Problem" by kind permission of the publishers, Messrs. Hurst & Blackett.

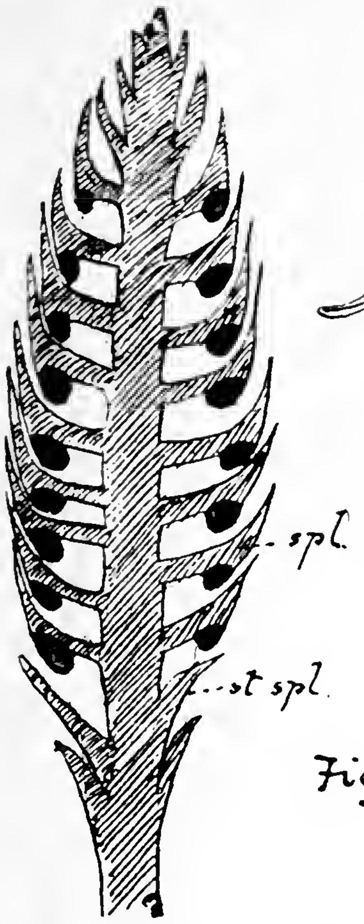


Fig. 1, Cone of Cycas.

Fig. 2, Myosurus

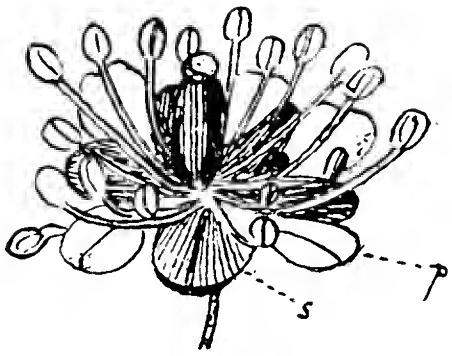


Fig. 3, Actaea spicata.

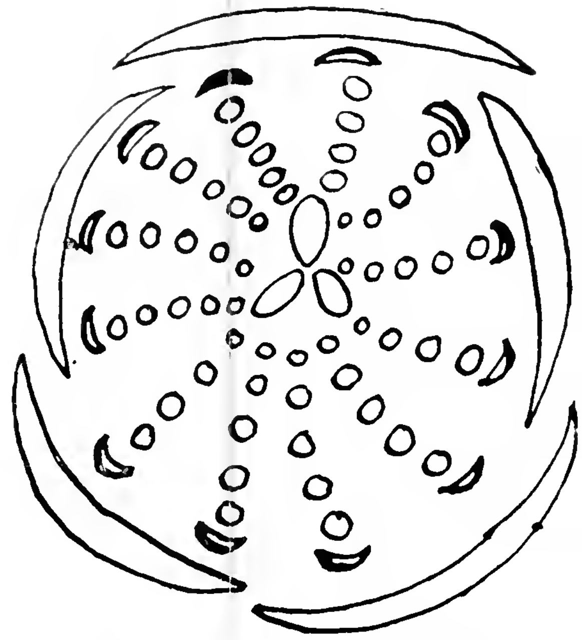


Fig. 4, Hellebore

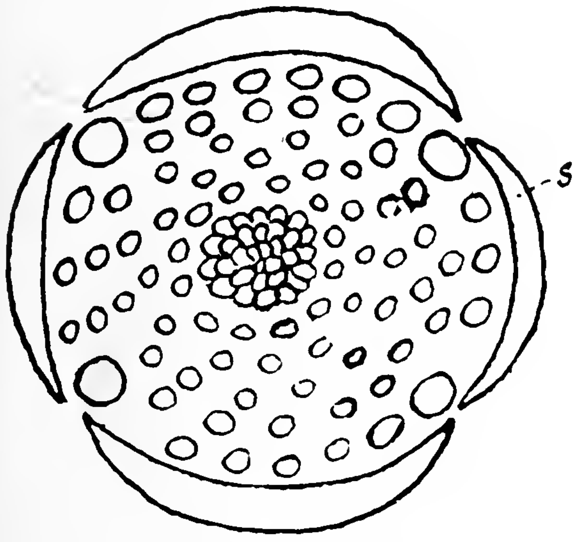


Fig. 5, Clematis integrifolia

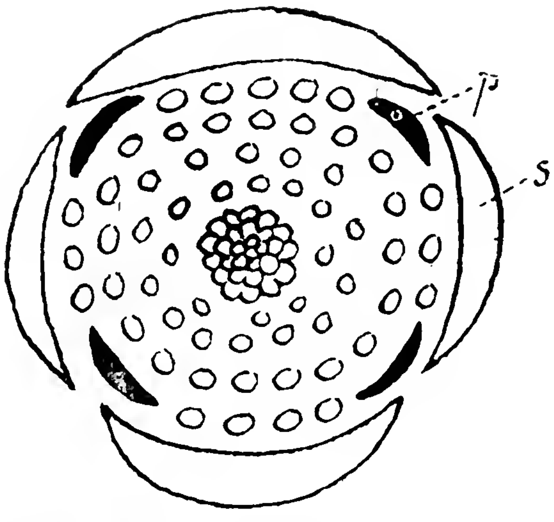


Fig. 6, Atragene calycina

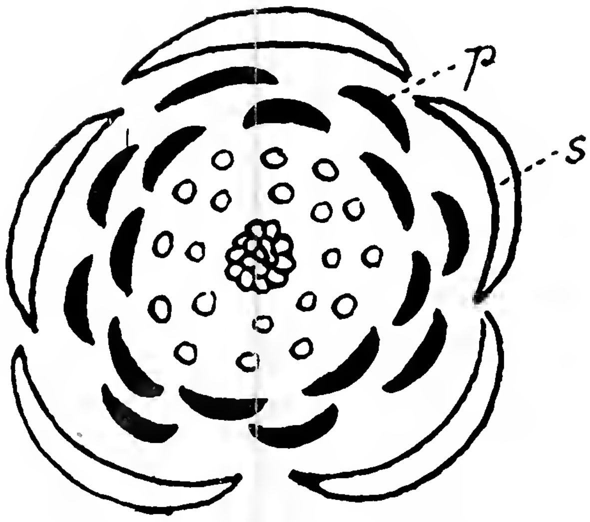


Fig. 7. Adonis vernalis

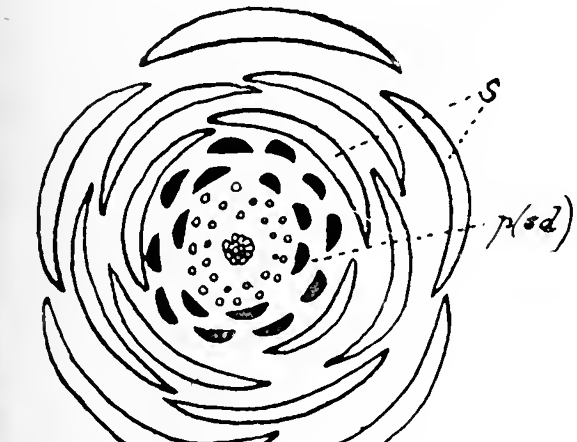


Fig. 8. Trollius europaeus

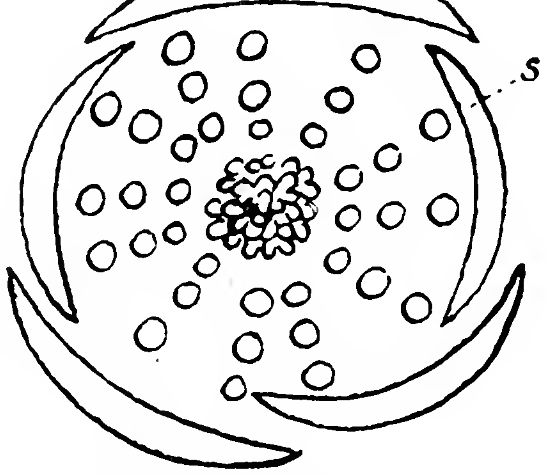


Fig. 9, Anemone ranunculoides

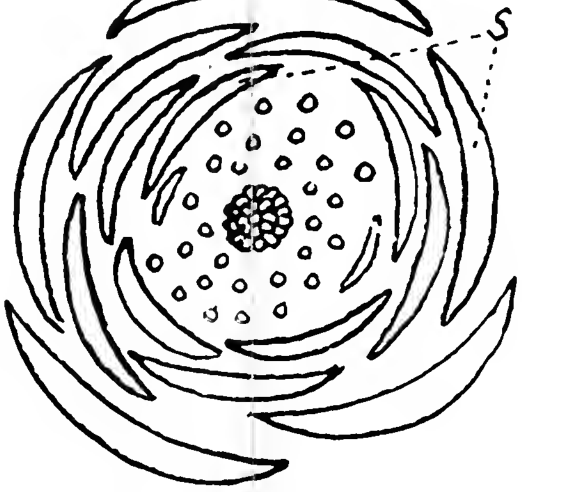


Fig. 10. Anemone japonica

N. C. W. del.

THE ORIGIN OF THE PERIANTH OF FLOWERS.

vegetation is an example of a *transitional flora*, formed upon alluvial soil or recent lake-deposits, a flora, that is, which is at the present moment colonising soil from which the water has only recently receded, and which will in course of time pass over into regular forest.

This solution first presented itself to Mr. Moore during a march from the forests of the Upper Semliki valley to the shores of the Albert Nyanza. The whole journey was over plains of alluvium and lake-deposits which showed that the lake once extended over the entire area, but though thick forest covered part of the Semliki plains, this gave place northwards to park-lands, while, as the lake was approached, the park-lands were gradually replaced by steppe-country with very few trees and finally by "absolutely treeless salt wastes bordering the shores."

Mr. Moore's explanation of this series of phenomena is best given in his own words.

"By the lake shore there was a belt of reeds, and beyond this almost desert steppes over which the fierce tropical sun blazed without protection for many hours during during the day . . . . . . The surface of the earth was dessicated and sandy, but a few inches below there was an appreciable amount of moisture, due to the occasional storms which sweep over such plains and disappear almost as quickly as they form. Nothing but grass grew near the lake, and even this had evidently had a very bad time, for it was scraggy and white and bleached, and alternated with patches of absolutely bare sandy soil. On these plains there were, however, in places, scattered over the surface of the ground, a few young euphorbia trees, the seeds of which had evidently been disseminated over the plains by the wind or birds, and as these hardy plants grew bigger on the older land further from the lake shore, I noticed that in the hot glare of noon their massive structures threw a patch of deep cool shadow round their feet Farther away from the lake where the land was older and the euphorbias had consequently had time to grow proportionately bigger, the noon-day spot of shade had also correspondingly increased, and in the area of such shadow there were to be found varieties of plants, besides the grass, which here found protection from the fiery glare and heat, and were consequently able to grow. Among these plants struggling against the naturally adverse conditions of the plains under the euphorbia shadows there were thorn trees, climbing plants, and flowering shrubs, and when once these plants had got a footing on the plains they prospered like one of Germany's protected industries, and

throve amazingly; so much so indeed, that on land that was still further from the lake, and consequently still older, the thorns and bushes of various sorts were enveloping the euphorbias, which now appeared as rather choked growths in the centre of the bushy patches. Further away again from the lake there were many clumps of bushes and trees scattered in all directions over the country; and in many of these were still to be found the dead or dying remains of the original euphorbia, to the protection of which the bush patch owed its growth. The seven lean kine had here eaten up the seven fat kine, and in such districts we entered the typical scenery of an African park.

Once started the groups of trees and patches of bush which marked the graves of their former benefactors, the euphorbias, spread gradually under the protection of their own shadows, until finally the patches ran together and more or less coalesced into the ragged forest which covers the higher portions of these long alluvial slopes." (The Tanganyika Problem, pp. 114-117.)

Mr. Moore points out that at least in the regions which he visited park-lands were only found on recently formed alluvial plains, and that their occurrence had no relation to rainfall, since they "occur in the Semliki valley where it is very wet, and also on the Albert Edward plains where it is very dry" (p. 113). Further, he could find no trace in any instance of differences in the soil—either of dampness or other characters—between the spots where the clumps of trees were growing and the grass-covered stretches between. Though it is not definitely stated in the book, it also appears that the euphorbia which he found playing such an important part in the initiation of the Park-Lands of the Albert Nyanza plains, also occurs, and plays the same part, in the other Park-regions which he observed.

Of course further information on several points is much to be desired, but taken as it stands, Mr. Moore's theory is very convincing. Whether it can be applied to the West African Park-Lands is another matter; while in the cases of the great Savannahs of South America, and the striking Park-landscapes of North-Eastern Asia (Kamschatka and Saghalien), it is probable that we must look for some quite different explanation, possibly on the lines suggested by Schimper.

Through the courtesy of Mr. Moore and of his publishers, Messrs. Hurst and Blackett, we are able to reproduce a plate from "The Tanganyika Problem," illustrating the gradual development of Park-Lands (Plate II.) A.G.T.

THE JURASSIC FLORA OF BORNHOLM.

DURING the last few years botanists have been gradually, though slowly, realising the fact that the study of petrified plants is not a purely geological pursuit; but even now the importance of Palæozoic types as evidence bearing on problems of evolution and phylogeny receives but half hearted recognition. Slight as it is, however, the interest shown by the average botanist in morphological researches in Palæozoic botany is much greater than that with which he regards the work of those who attempt to interpret the imperfect records of Mesozoic floras. It is unfortunate that the great majority of plants obtained from rocks of more recent date than the Carboniferous and Permian epochs are not preserved in such a manner as to retain their internal structure, but to neglect post-Palæozoic fossils for this reason is to adopt a view at once, narrow and prejudicial to botanical progress. The determination of mere casts and impressions is naturally attended with considerable risk and offers strong temptation to ill-balanced imagination. It is notorious that the custom of applying the generic names of recent plants to fossil fragments, which exhibit an external resemblance to leaves and shoots of existing species, has not only been responsible for entirely false deductions but has brought into deserved discredit many contributions to palæobotanical literature. If on the other hand we disregard all fragmentary and indecipherable records we still find a large amount of material sufficiently well preserved to be assigned on substantial evidence to a definite family or generic position. It is not too much to expect that a careful examination of the remnants of the Mesozoic vegetation will reveal many facts of primary importance likely to supply trustworthy information as to the geographical distribution during past ages, which may enable us to follow the changes that have resulted in the present balance of power in the plant world.

A recently published paper by Hjalmar Möller[1]—a new worker in the domain of Palæobotany, trained by Professor Nathorst of Stockholm—On the Pteridophytes of Jurassic age from Bornholm, is a good example of a careful systematic account of a flora of considerable interest. Without discussing certain statements and determinations which are open to criticism, it may be of interest to draw attention to a few conclusions to be drawn from the investigations of Möller, and those previously published by

[1] Bidrag till Bornholms Fossila Flora. *Kongl. Fysiog. Sällsk. Handl.* Bd. XIII. *Lund*, 1902.

Bartholin,[1] on this northern type of Jurassic vegetation. The Flora in question is undoubtedly of Jurassic age, possessing many features in common with the rich flora from the inferior Oolite rocks of the Yorkshire Coast and containing several elements suggesting a comparison with the older Rhætic floras of Scania and Franconia.

A comparison of Rhætic and Inferior Oolite floras demonstrates a close agreement as regards general composition between the vegetation of these two periods of the Mesozoic epoch. Among the Bornholm ferns we find an example of the Marattiaceæ, a family no longer existing in the European region; several representatives of the Dipteridinæ, a section of ferns containing the single surviving genus *Dipteris* which is practically confined to India and Malaya. The Matonineæ, another family of ferns with the solitary living genus *Matonia*, restricted to the Malay Peninsula and Archipelago, is represented by specimens hardly distinguishable from the recent species *Matonia pectinata*. Numerous Cycadean fronds point to the prominent place in the Jurassic vegetation of Northern Europe occupied by extinct forms of a group now confined to the tropics, and consisting of a mere handful of more or less rare species. The existing Maiden-Hair tree—a type that perhaps no longer occurs as a wild plant—is another illustration of an ancient stock (the Ginkgoales), which has left clear traces in the Bornholm rocks. The Coniferæ, often among the least satisfactory of fossil plants, are for the most part represented by fragments of vegetative shoots only, and cannot be determined with certainty. We notice, however, that such forms as occur do not agree in their vegetative character with the existing Abietineæ, a section of the Coniferæ which appears to be of more recent origin than the Araucarieæ and other families.

A.C.S.

[1] Nogle i den bornholmske Juraformation forekommende Planteforsteninger. *Bot. Tidsskrift*. Bd. XVIII. and XIX., *Copenhagen*, 1892-94.

THE LONDON BOTANICAL SOCIETY.

THE Botanical Society founded by Professor Farmer some three or four years ago for the more or less informal communication and discussion of the preliminary results of work done by its members, and of any other matters of botanical interest, steadily continues its useful career. Its meetings are usually held in the Biological lecture-room at the Royal College of Science, South Kensington, once in every month during the working year, and it is thought that short reports of the proceedings may interest the readers of the NEW PHYTOLOGIST, and Professor Farmer's consent having been obtained, a brief outline of the meetings will in future

be given. The substance of papers read will not be reported without the express consent of the readers.

The first meeting in 1903 was held on Tuesday, January 20th, at 4.30 p.m., Dr. D. H. Scott in the Chair. Mr. A. G. Tansley gave an account of the "Vascular System of *Matonia pectinata* and its relation to those of other Ferns." The account embodied the results of work, mainly carried out by Miss R. B. Lulham at University College, on material collected by Mr. Tansley on Mount Ophir in Johore, Malay Peninsula (the classical locality for the comparatively rare fern *M. pectinata*), in January, 1901. Reference having been made to Mr. Seward's original description of the anatomy of the rhizome and petiole (Phil. Trans., 1899) and Miss Wigglesworth's discovery that the rhizome may contain three concentric "amphiphloic siphonosteles" (New Phytologist, July, 1902), it was shewn that all transitional cases may occur in the rhizome of the mature plant between a vascular system composed of two and one composed of three concentric siphonosteles. From a preliminary investigation of the young plants, it appears that the first formed portion of the stem contains a single solid "protostele," which becomes medullated at a higher level. From the interior of this a second protostelic strand is nipped off, and this, coming into connexion with the primary stele at the nodes, gradually passes through the "*Lindsaya*-phase" into the siphonostelic condition. The two concentric siphonosteles thus obtained may exist alone in the mature rhizome, but frequently a third strand is nipped off from the interior of the second, or arises freely in the pith. This may remain protostelic, it may pass into the "*Lindsaya*-phase," or it may itself become siphonostelic.

The rest of the account was devoted to a consideration of the nodes, of which 35 had been examined. The typical structure was made clear by means of drawings of a solid model of the vascular system, and the exact relations of the three steles to the leaf-trace elucidated. A theory of the gradual evolution of this from the simple curved leaf-trace characteristic of ferns possessing a single siphonostele in the stem, in connexion with the evolution of the two inner steles and in accordance with the transitional structures found in the young stem, was put forward, and its probable physiological causes outlined. Finally a fundamental similarity was suggested between the course of evolution in *Matonia* and the other ferns having a "polycyclic" arrangement of vascular strands in their stems, e.g. *Saccoloma*, Cyatheaceæ, Marattiaceæ, etc., the general view being that the additional internal strands are always primarily "compensation-strands" (Ersatzstränge). Mr. L. A. Boodle, Mr. C. E. Jones and Dr. Scott took part in the discussion.

THE ORIGIN OF THE PERIANTH OF FLOWERS

With Special Reference to the Ranunculaceæ.

[Plate III.]

CASPAR FRIEDRICH WOLFF[1] was the first to hint at the origin of the flower as being the outcome of a gradual metamorphosis of the foliage-leaves situated at a lower level on the axis of the plant. He held that the production of floral leaves was the result of a degeneration in the quality of the sap, the richer portion being used up at a lower level by the first-formed vigorous foliage-leaves. Goethe[2], however, first established the theory of the underlying homology of all foliar organs of the plant. His main idea was that the floral leaves represented the final stage in a gradual ascending metamorphosis of which the foliage-leaves are the starting-point, and that the production of flowers is due to an improvement and etherealisation of the sap during its ascent through the plant. All foliar organs are variants on an ideal type-leaf. These two great thinkers dealt solely with the individual development of the plant; they, like so many biologists since their time, failed to see that this could throw no real light upon the ultimate phylogenetic development of the parts concerned.

Goebel[3] states that the type of which all foliar organs are the modifications is the *foliage-leaf*, a view sufficiently idealistic and resembling Goethe's "type-theory."

We hold, for cogent reasons[4] which it is beyond the scope of this article to enlarge upon, that fertile foliar organs (or sporophylls) preceded in time all other kinds of leaves, and that the latter have been gradually differentiated from the former by a process of sterilisation of their tissues.

[1] Wolff, C. F. Theoria Generationis, 1759.

[2] Versuch die Metamorphose der Pflanzen zu erklären, Gotha, 1790 ("Essay on the Metamorphosis of Plants;" translated by Emily M. Cox in Seemann's Journal of Botany, Vol. I., 1863).

[3] "Die vergleichende Entwickelungsgeschichte der Pflanzenorgane;" Schenk's Handbuch der Botanik, Vol. III., part 1, p. 100, 1884.

[4] See *Celakovsky*: "Ueber die allgemeine Entwickelungsgeschichte des Pflanzenreiches;" Kgl. böhm. Gesellsch. der Wissenschaften; Naturwiss.-Mathem. Section, 1868.

"Ueber den phylogenetischen Entwickelungsgang der Blüthe, etc., part 1, p. 7, loc. cit., Prag, 1896.

"Ueber den phylogenetischen Entwickelungsgang der Blüthe, etc., part 2, p. 162, Prag, 1900.

"Nachtrag zu meiner Schrift über die Gymnospermen;" Englers Bot. Jahrbüch, etc., Vol. XXIV., part 2, 1897.

Epilog zu meiner Schrift über die Placenten der Angiospermen;" (appendix) Sitzungsb. d. Kgl. böhm. Ges. d. Wiss., 1899.

Now we must look for the nearest origin of our modern flower to the *cone* of the Cycadaceae, which is, in fact, the primeval flower consisting of a much-elongated axis clothed with very numerous spirally-arranged sporophylls. But the chief point of interest lies in the fact that in all cases a few of the lowermost sporophylls are perfectly sterile and somewhat altered in shape, although not in texture or colour, from the fertile ones. They may, in fact, be regarded as the progenitors of the perianth-leaves of the Angiosperms. And it is obvious that they have been derived by *simple sterilisation of the lowermost sporophylls* of the cone. (Fig. 1).

We may, in tracing from this point onwards, the evolution of the flower, confine our attention almost exclusively to the order Ranunculaceæ among the higher plants, as there is a great deal of nstruction to be gleaned from this group. Here we find some of the primitive characters of the cone still present: *e.g.* inconstancy and indefiniteness in the number of members of the various categories of floral foliar organs (not yet stereotyped into the 5's or 4's or 3's of the more advanced orders); the much-elongated floral axis, as seen especially in *Myosurus* (Fig. 2) and also in an allied order, the Magnoliaceae. The new, more advanced characters which have appeared are:—the coloration of the perianth (yet exceptions to this occur), and the frequent addition of an extra category or whorl of perianth-leaves to that already present. Having recognised these features we will first of all enquire into the origin of the *corolla*. Nägeli[1] and subsequently Drude[2] were the first to point out the probable origin of the corolla from the outermost whorl of stamens. Not long afterwards Grant Allen[3] ingeniously endeavoured to prove that the petals of flowers are in all cases derived from stamens. With the last-named authors he considers the calyx to have been derived from bracts. The great German botanist Prantl[4] held, on the other hand, that the corolla, like the calyx, arose from the metamorphosis of *bracts*, and that *staminodial* structures only (including *nectaries* and small petaloid organs bearing incomplete or rudimentary anthers) had been transformed from the outermost stamens. Having especial regard to the Ranunculaceæ, he always drew a sharp distinction between these staminodes on the one hand and the corolla on the other. For instance, he regards the nectar-bearing "petals" of *Ranunculus* as staminodes and possessing a totally

[1] Mechanisch-physiologische Theorie der Abstammungslehre; p. 496 1884.

[2] "Die systematische and geographische Anordnung der Phanerogamen;" Schenk's Handbuch, Vol III., part 2, 1887.

[3] The Colours of Flowers, 1882.

[4] "Beiträge zur Morphologie and Systematik der Ranunculaceæ;" Engler's Bot. Jahrbücher, Vol. IX., 1887.

different origin from true petals. He ascribes to *Actaea*, along with *Cimicifuga*, the universal possession of staminodes. Celakovsky, from whose works all that this article contains is gleaned, is of opinion that the sharp distinction made by Prantl cannot well be maintained; for instance, the tiny petals of some species of *Actaea* (*Euactaea* Prantl) are without nectaries, while others (*Cimicifuga*) produce them; the same holds good for *Coptis*. Further, the fact that many petals not possessing nectaries, and to which Prantl assigned the character of staminodes, exhibit rudiments of anthers, while the petals of *Adonis* do not is of no decisive importance, for such transitional forms between stamens and petals do not occur in all species of those genera to which staminodes are ascribed, as is the case in our own *Actaea spicata* (Fig. 3). It is, therefore, far from clear why these latter should have been derived from stamens and the petals of *Adonis* enjoy a different origin. Other important facts, for which there is no room here, tend to render Prantl's view improbable. And we have only to turn to any "double" flower in the garden to observe the *gradual transitions* taking place under our very eyes, between stamens and true petals to be convinced that staminodes and petals have precisely the same origin, and that what to-day occurs abnormally may have been phylogenetically the normal process.

We have hitherto assumed that staminodes are of staminal origin; the real *raison d' être* of this view lies in the fact that *nectaries* usually exhibit a more or less distinct 2-lipped structure, the upper (inner) lip being homologous with the *upturned basal lobe of a peltate anther*,[1] while the non-secretory staminodes very frequently bear rudiments or portions of pollen-sacs.

Without entering further into the question we may conclude with Prantl that nectaries and other staminodes are of staminal origin; but it seems quite permissible to proceed farther and add that in the same way as the petals of *Ranunculus* and *Callianthemum* have been derived from the expansion and enlargement of the *outer* or *lower lip* of the nectaries (*e.g.*, of *Helleborus* (Fig. 4)—so also the petals of *Adonis* have been derived from small pollen-bearing or sterile staminodes and, therefore, ultimately from stamens.

A very pretty piece of evidence in favour of the view just stated—that petals are of staminal origin—can be adduced from the behaviour of the flowers in the *Clematis*-group. The perianth of most species of this genus is single and of the nature of a *calyx*; within, the numerous stamens are spirally arranged. In *Clematis integrifolia*,

[1] This is shewn by Celakovsky as a result of his investigations into the origin of the perianth of *Narcissus* as seen in the phenomena presented in many double flowers of that plant.

according to Eichler, four of the stamens, *viz.*, the outermost ones, are conspicuously larger than the rest, and, moreover, alternate regularly with the four sepals (Fig. 5). Now, if we turn to the species *C. balearicus* (*Atragene calycina*) the four large stamens of the last species are exactly replaced by *four small petals* (Fig. 6). Eichler observed in cultivated specimens of *Atragene alpina* that not only were the four large stamens of *C. integrifolia* replaced by petals, but that also all the intervening stamens belonging to the same spiral cycle as the four large ones, as well as the whole of those of the next inner cycle, had become transformed into tiny petals; the four alternating with the sepals considerably exceeding in size any of the other stamens.

Now what has here in *Atragene alpina*, been noticed as an abnormal phenomenon occurs *normally* and typically in *Adonis vernalis* where, to the 8 petals succeeding the sepals, and which are alone present in *A. autumnalis*, is added a second inner whorl of 8 or, more frequently, a slightly larger number of petals (Fig. 7). In *Adonis aestivalis* and other annual species 6, 5, or even fewer petals are present; thus the remaining petals, which, in *A. autumnalis* make up the 8-merous character of the corolla, occur here as stamens. There seems, at least to our mind, little doubt in these cases as to the origin of the petals. Other similar cases could be cited. But what we have written is probably sufficient to demonstrate the origin of the corolla from the andrœcium.

Let us now turn to the *calyx* and try to discover its region of birth. It is a striking and beautiful fact, as illustrating the division of labour that takes place in the economy of the flower in this group of plants, that in the absence of a double perianth, the single one (which, on the analogy of the flowers of the great generality of plants, must necessarily be regarded as a calyx) assumes the characters, *viz.*, the colour and texture, of the corolla in the double perianth. Such a petaloid calyx is exhibited by *Caltha*, *Trollius palmatus*, *Isopyrum* (sect. *Enemion*,) *Trautvetteria*, *Clematis* sp., *Anemone* sp. (Fig. 9), *Thalictrum* sp., *Hydrastis*. As regards the generality of its species, *Trollius* is in this respect an interesting genus. Its corolla consists of small staminodial structures; the outermost of these have, on Celakovsky's view, been transformed at some time or other in the past history of the plant into *extra* sepals, so that in *T. europaeus*, *T. asiaticus*, etc., the petaloid calyx, unlike its 5-merous counterpart in the white-flowered *T. laxus*, has become polymerous (Fig. 8).

Now, we have to decide which is the more *primitive*: the ordinary *green* calyx of *Ranunculus* and the majority of Dicotyledonous plants, or the *petaloid* calyx of the cases just mentioned.

Celakovsky points out the following facts as proving the latter to be the original form. When a typically coloured corolla is present the calyx is usually, or very often, green and bract-like; when the corolla is represented by inconspicuous nectaries or staminodes the calyx is seen to exhibit the attractive characters typical of the petals. This latter fact is aptly and beautifully illustrated in the relation which a South American species of *Ranunculus*, *R. apiifolius* Pers. (*Aphanostemma*), holds to the other species of the genus. In most species, as in *R. acris*, a well-developed coloured corolla is present, and the calyx is green; but in the South American species the petals are represented by extremely small, sub-bilabiate staminodial structures greatly resembling the nectaries of *Xanthorrhiza*, while, in distinct correlation therewith, the calyx is more or less petaloid in character. The occurrence of a similar petaloid calyx in conjunction with a staminodial corolla is seen in many species of *Helleborus* (*H. viridis* and a few others, with their green calyx, furnishing an exception to the rule), in *Nigella*, *Eranthis*, *Xanthorrhiza*, *Coptis*, and very strikingly in *Delphinium* and *Aconitum*, where the (in most cases) blue-coloured *calyx* admirably simulates, in its zygomorphic character and adaptability to the visits of insects, the highly modified zygomorphic *corollas* of many of the more advanced orders of plants.

Now, on the view we are considering, the staminodes are necessarily of earlier origin than the typically coloured petals because more nearly related to the stamens, and derived from the latter; hence it follows that the petaloid calyx (the almost constant accompaniment of these staminodes) must be of earlier origin than the green calyx of *Ranunculus acris*, &c., and that of most Dicotyledons.

Finally, we may call into view another set of phenomena which are exhibited by the interesting genus *Anemone*. Our own observations shew that in some species, as *A. virginiana*, *A. pennsylvanica*, and *A. ranunculoides* there is a single perianth-whorl of five coloured leaves, these being arranged, as in *Calthæ*, &c., in a two-fifth spiral (fig. 9), the perianth is thus in this case, as in the other genera above mentioned, obviously a calyx. In other species, as *A. hortensis*, *A. nemorosa*, *A. Halleri*, there is a distinct tendency shewn towards the arrangement of the sepals in two distinct whorls, while at the same time one or two extra sepals have been added above, with the result that there obtain, as in the Common Wood Anemone, two whorls of three or four members each. *A. sylvestris* affords a transitional case, where the five sepals are, as it were, hesitating whether to be whorled or spirally arranged on the axis,

Now consider the very striking case of *A. japonica* or of *A. stellata*. Here, to the original and primitive 5-merous calyx, a considerable number of members have been added, so that the perianth frequently consists of as many as twenty sepals,[1] and it is, moreover, clear that these have been added from the stamens, by metamorphosis of the latter, for, in the centre of the flower, transitional forms between stamens and sepals are always present and we receive, as it were, ocular demonstration of the method of production of these sepals which from without inwards form a continuous spiral of similarly-constituted petaloid leaves (fig. 10). But the most important fact has yet to be stated. In *A. japonica* two or three of the outermost sepals (as is also the case in *Trollius*) are always slightly differentiated from the rest, owing to their having, in whole or in part, a somewhat darker, purplish coloration,[2] and occasionally they exhibit a decidedly *greenish* tinge. Now, in that section of the genus known as *Knowltonia* (exhibiting also a polymerous calyx) these *two or three outermost sepals are entirely green and bract-like*. Prantl accounts for the polymerous perianth of these forms by assuming that the single perianth of other species (which, on his view, is of bracteal origin), first multiplied its parts and subsequently became differentiated, as regards colour and texture, into two distinct portions. But, as Celakovsky aptly suggests, this multiplication could hardly have taken place *ex nihilo*; on the contrary, the extra sepals must necessarily have been derived by metamorphosis of the stamens; and further, if the perianth be originally of bracteal derivation it would seem strange that single perianths of a green bract-like consistence are of such rarity in the order. But, as regards this, and all other questions bearing on the subject of this article, we leave our readers to judge of the respective value of the theories of the two authors whose names have been chiefly introduced. Yet after all the impressive facts above detailed it seems to our mind fairly clear that in the great order Ranunculaceae, calyx and corolla have sprung from the self-same source, viz. the *andrœcium*; that they constitute one and the same morphological structure, which, following the economic needs of the plant, appears now as green protective leaves, now as brightly-coloured, delicately-textured organs for the allurement of insects which are the destined agents in the fertilization of the flower.

And if this be the history of the evolution of the perianth in the group of plants we have been considering, it is surely but

[1] The same phenomenon exists normally in the genus *Clematis*, in such species as *C. florida* and *C. patens* where the calyx may consist of as many as ten sepals.

[2] In the polymerous calyx of *A. rivularis* we have noticed that the five outermost sepals are of a dark purple colour below.

rational to conclude that the same story will be true of all other groups of flowering-plants as well. Celakovsky, from the investigation of certain double flowers of *Narcissus*, found every transition occurring between the stamens and the members of *both* perianth-whorls, showing how, in fact, the "corona" or "trumpet" represents the upturned basal lobe of a peltate anther, each member of the perianth possessing such an appendage. If this be true for *Narcissus*, it must necessarily hold good also for the perianth of *all other* Monocotyledons, including such a differentiated type as that of the Alismaceæ or the Commelynaceæ.

Hence we see that everywhere both calyx and corolla may lay claim to a similar place of birth, viz., in the andrœcium, however distinct and dissimilar from each other in almost every character they may at times appear.[1] W. C. Worsdell.

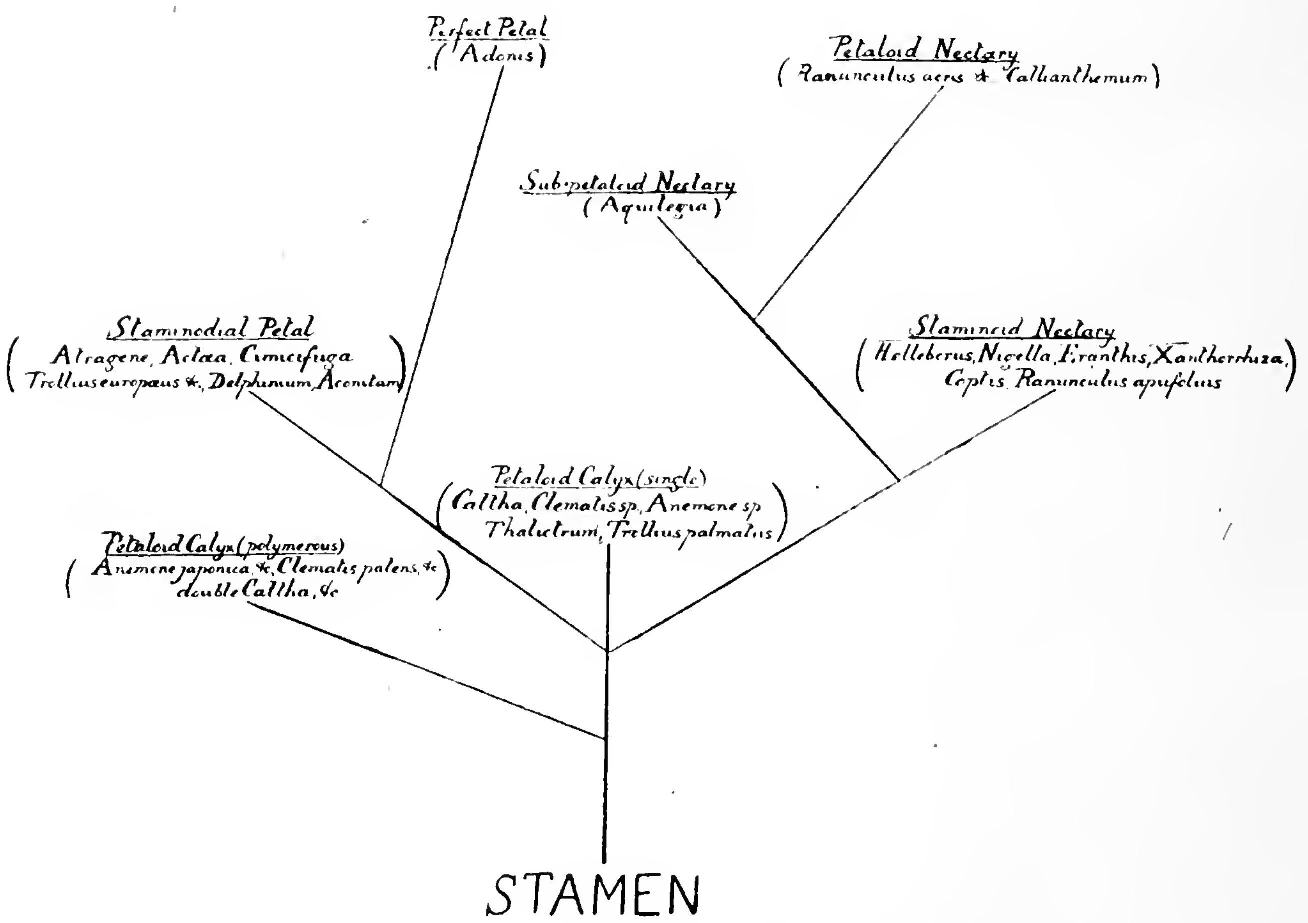


DIAGRAM ILLUSTRATING ORIGIN OF CALYX AND COROLLA.

s = sepals. p = petals. n = nectaries. sd = staminodes
spl = sporophyll. st.spl = sterile sporophyll.

[1] In *Calycanthus* the most gradual transitions occur from the stamens downward through the petals and sepals to the bracts.

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NOTES ON FOSSIL FUNGI.

By F. W. OLIVER.

OF the various classes of plants of which structural remains are known from the Palaeozoic rocks, the Fungi would seem to have been the least fully studied. And this is hardly surprising in view of the attractions to investigation which the vascular plants offer. Some day, skilled mycologists will direct their attention to this promising field of study and we shall be able to realise, as we now do in the case of the Pteridophytes and Gymnosperms, what were the relations of the fungus-flora of that period to the group as it now exists. Meanwhile it is possible, as in the present instance, to place on record detached observations concerning some stage in a life-history. The present notes deal with two types of reproductive organ, both of which have been noticed by the French Palaeobotanists.

A Fungus on the pinnules of ALETHOPTERIS AQUILINA, Schlotheim.

The first case to which attention is drawn is that of the curious ovoid pockets occasionally met with in the pinnules of *Alethopteris aquilina.* The fern-like foliage which has received this name is regarded as having belonged to one of the Medullosas, and as the constant lack of sori on these and many other fronds of the older rocks has tended to strengthen the suspicion that these plants may have borne reproductive organs unlike those of true Ferns, a close scrutiny is desirable of any structure which might be construed as a possible sporangium. The pinnules of *Alethopteris aquilina* are quite common in the silicified nodules of permo-carboniferous age at Grand 'Croix, whence the specimens under consideration were derived.

The pockets in question (diameter about ·2 mm.) were described by Renault[1] as lying between the forkings of the lateral veins of the

[1] Renault: Cours de bot. fossile III, 1883, pp. 159-'60 and Pl. xxvii, fig. 10.

pinnules. In this writer's figure of a section parallel to the surface of a pinnule the pockets shew an oval outline, they are slightly variable in size, and contain numerous small spore-like bodies. A comparison of the similar preparation represented here (Pl. iv., fig. 1) with Renault's fig. 10, will shew the identity of the structures. In his comments on their nature Renault refers in the most guarded terms to the possibility that these pockets might be the sporangia of *Alethopteris*. On the whole he would seem to have been impressed with the resemblance which they present to *Excipulites callipteridis* of Schimper.[1]

The specimens under consideration afford some additional features worth recording. The irregular distribution of the pockets finds confirmation in the cross sections of pinnules represented in figs. 2 and 3. In the former figure, which represents part of the lamina of a pinnule in transverse section (the midrib being on the extreme right of the figure), four of these pockets (*a*, *b*, *c*, *d*) are shewn lying in the areas of spongy parenchyma which alternate with the exarch bundles of the pinnule. They are closely approximated to the lower surface of the leaf which projects slightly in the form of convex blisters owing to the displacement due to the pockets. Another pinnule in transverse section is shewn in fig. 3 with two pockets (*a* and *b*), one close to the midrib, the other in the angle formed by the infolding of the rolled margin. These two pockets, like *a* and *d* in fig. 2, appear to have been cut in the middle plane and shew an ostiole-like aperture through which the contained spores were probably discharged. The wall of the pocket is badly defined. It is dark in colour and under a high magnification shews an obscure stratification (fig. 4). The appearance certainly suggests that this wall may owe its origin to the flattening of the neighbouring parenchyma cells of the leaf, a result of the expansion of the pocket. The small contained spores are not quite spherical, their longer diameter averages about 16μ. The wall of the spore is covered externally by numerous tiny rugosities, as represented in fig. 5. The general facts of their structure and distribution seem consistent with the view that these pockets are the fructifications of a parasitic fungus. Superficially they recall a minute Pyrenomycete, but no useful purpose would be served by a discussion of its possible affinities. The manner of origination of the spores in the pockets is quite an open question. A portion of the wall of a pocket together with some of the adjacent spores are represented in fig. 4. The details

[1] See Schimper, Traité d. paléont. végét., Vol. I., p. 142 and Pl. xxxii., figs. 6 and 7.

of the structure of the wall are obscure, though there is some slight ground for believing the pocket to have possessed a lining of hyphae. The state of affairs figured here, of spore-like bodies arising from hyphae, is brought forward with some reserve, as this stage has only been seen in a single instance.

When all the facts are taken into consideration, the distribution and form of the sacs, the smallness of the spores, and the ill-preserved character of the tissues generally in these specimens, there would appear little room for doubt as to the fungal nature of the pockets. What may have been the affinities of the fungus and its relations to recent parasitic fungi are questions that must be reserved till our knowledge of the Palaeozoic Fungi is more comprehensive than at present.

On certain supposed Chytridineous Sporangia.

The other fungi receiving mention here come from the same horizon and present a close resemblance with *Grilletia Sphaerospermii* described by Renault and Bertrand[1]. The latter was met with in the peripheral layers of the nucellus of the seed *Sphaerospermum* in which hyphae and strings of sporangium-like vesicles suggested a reference to the Chytridineae. This same type of vesicle has been found in considerable quantity in Brongniart's seed *Polylophospermum*, occupying the same position as in Renault and Bertrand's example. The beak-like processes represented in two of the vesicles of the series of three in fig. 6 and in fig. 6a, marks, no doubt, the place of dehiscence. Though this specimen is less complete than that described by the French authors, for the hyphal threads are not preserved, there seems little doubt as to its identity. Fungal structures of this kind occurring in the wall of the nucellus of palaeozoic seeds were not limited to this particular horizon, as almost identical structures have been observed in a specimen of the seed *Conostoma* from the calciferous sandstone series of Burnt Island in Scotland (Lower Carboniferous). The vesicles of the *Grilletia* from *Polylophospermum* vary in diameter from 25μ to 40μ. They appear to have been approximately spherical in form, whilst dehiscence occurred by rupture at the tip of the beak rather than by the removal of an operculum. This was inferred in the case of MM. Renault and Bertrand's specimens from the fact that many of the sporangia had opened at this point.

Another example of possible Chytridineous sporangia is that of

[1] Renault and Bertrand, *Grilletia Sphaerospermii*, Chytridiacée fossile du terrain houiller supérieur. Comptes Rendus, tom 100, p. 1306.

certain dubious structures recently found in the surface layers of the nucellus of what is probably a second species of *Stephanospermum*.[1] The bodies in question lie at the surface of the nucellus everywhere between the pollen-chamber and the chalaza. The sketch of part of a tangential section of the nucellus of this seed (Fig. 7) shews the nucellar epidermis (*e*) detached from the underlying parenchyma (*np*) within which follows the tracheal mantle (*t*). Finally the wall of the macrospore (*mw*). Lying here on the nucellar parenchyma are these small ovoid bodies (*a*, *b* & *c*) which are perhaps referable to a fungus like *Grilletia*. The average dimensions of these little vesicles is $23\mu \times 16\mu$. Further details of their structure are given in figs. 8, 9 and 10. Each vesicle is of ellipsoidal outline and shews a considerable degree of flattening upon the nucellar parenchyma. The examples represented in figs. 8 & 10 are typical. Each is represented lying on the crushed parenchyma of the nucellus, whilst a portion of a tracheide is also given in fig. 8. In the middle of the convex face of the vesicle an oval area is generally present symmetically divided along its major axis by a slit-like line (figs. 8 and 10). The bodies by themselves are difficult of interpretation, especially as no traces of connecting hyphae are present. Until the frequency with which *Grilletia*-like fungi occur in this actual situation was realised, it seemed possible the bodies might even belong to the nucellus. However, the most reasonable view of their nature seems to be that they are the sporangia of some fungus of similar nature.

A comparison has been drawn between *Grilletia* and the Chytridineae. If we turn to that group, forms are not lacking in which the sporangia bear specialised opercula connected with the discharge of the swarm-spores. This is the case for instance in the genera *Chytridium*, *Tetrachytrium* and *Zygochytrium*.[2] The curious pore-like appearance seen on these vesicles may possibly indicate the presence of an operculum which has become, perhaps owing to the confined position, partly pressed into the sporangium. One of these bodies is represented in fig. 9 with its convex surface partly ground away. The slit-like furrow (?) is still apparent, so that it may be inferred that this portion of the mechanism projected an appreciable distance into the vesicle. The whole structure, it may be conjectured, was a sporangium with an operculum of oval contour, in which, owing to the circumstance of its development,

[1] *S. caryoides*, as yet undescribed, also from Grand 'Croix.

[2] Schröter, Chytridineae in Engler and Prantl, Die natürlichen Pflanzenfamilien, I Teil, 1 Abt., pp. 80, 84 and 87.

the more or less conical lid being prevented from projecting out wards had become invaginated into the cavity.

DESCRIPTION OF THE FIGURES ON PLATE IV. ILLUSTRATING F. W. OLIVER'S *NOTES ON FOSSIL FUNGI.*

FUNGUS ON *ALETHOPTERIS.*

Fig. 1.—Section of a portion of a pinnule of *Alethopteris aquilina* cut parallel to the surface. At *a* one of the pockets filled with fungal spores is cut through. × 50.

Fig. 2.—Vertical section of part of a pinnule; the midrib is on the extreme right. *a*, *b*. *c* and *d*, the receptacles of the fungus. × 20.

Fig. 3.—Cross-section of another pinnule; *a* and *b* fungal receptacles. × 20.

Fig. 4.—Part of the boundary wall and a few spores from one of these receptacles. The spores appear to be attached to hyphae coming from the wall. × 625.

Fig. 5. A single spore. × 1250.

FUNGAL SPORANGIA FROM SEEDS.

Fig. 6.—Three sporangia in series, from the nucellus of *Polylophospermum* resembling those belonging to *Grilletia*, Renault and Bertrand. × 600.

Fig. 6a.—Another detached sporangium from the same source.

Fig. 7.—Portion of the wall of the nucellus of *Stephanospermum caryoides* cut in longitudinal tangential section. *mw*, wall of macrospore; *t*, tracheal sheath of nucellus; *np*, remains of parenchyma of nucellus; *e*, nucellar epidermis; *a*, *b*, *c*, supposed sporangia of a *Grilletia*-like fungus. × 85.

Figs. 8, 9, 10.—Three examples of the supposed sporangia, 8 and 10 shew the oval operculum with its characteristic furrow (*a*); in 9 the supposed operculum appears to have been ground away, but traces of the furrow remain. The cells upon which the oval bodies lie belong to the parenchyma of the nucellus. × 850.

A CONVENIENT FORM OF POTOMETER.

[Text-Fig. 1.]

THE apparatus that forms the subject of this note does not lay claim to any special originality, and is merely a convenient modification of a form that I have used for a number of years.

The corked bottle is provided, preferably, with an india-rubber cork with three holes bored through it. One of these takes the bent glass tube (T) which has a fairly fine tubulus, such as is ordinarily used for a potometer. It is important that this tube should not project beyond the lower surface of the cork, as otherwise any air that may accumulate, or be present, above the water inside the bottle cannot easily be got rid of.

The middle hole is destined to receive the stem of the shoot of which the rate of transpiration is to be measured, whilst the right-hand hole allows a thistle funnel (F), provided with a stopcock, to pass through it.

The chief advantage in the rubber cork lies in the ease with which the plant stem can be passed through it without injury, and gripped so as to be air tight. In order to do this, a blunt cork-borer smeared with oil or vaseline, and somewhat larger than the diameter of the hole is worked through it. The shoot is then passed into the tube of the cork-borer, and the latter withdrawn. The stretched rubber contracts upon the stem and if a shoot of appropriate thickness has been chosen, a perfectly air-tight enclosure is the results as soon as the cork is compressed by the

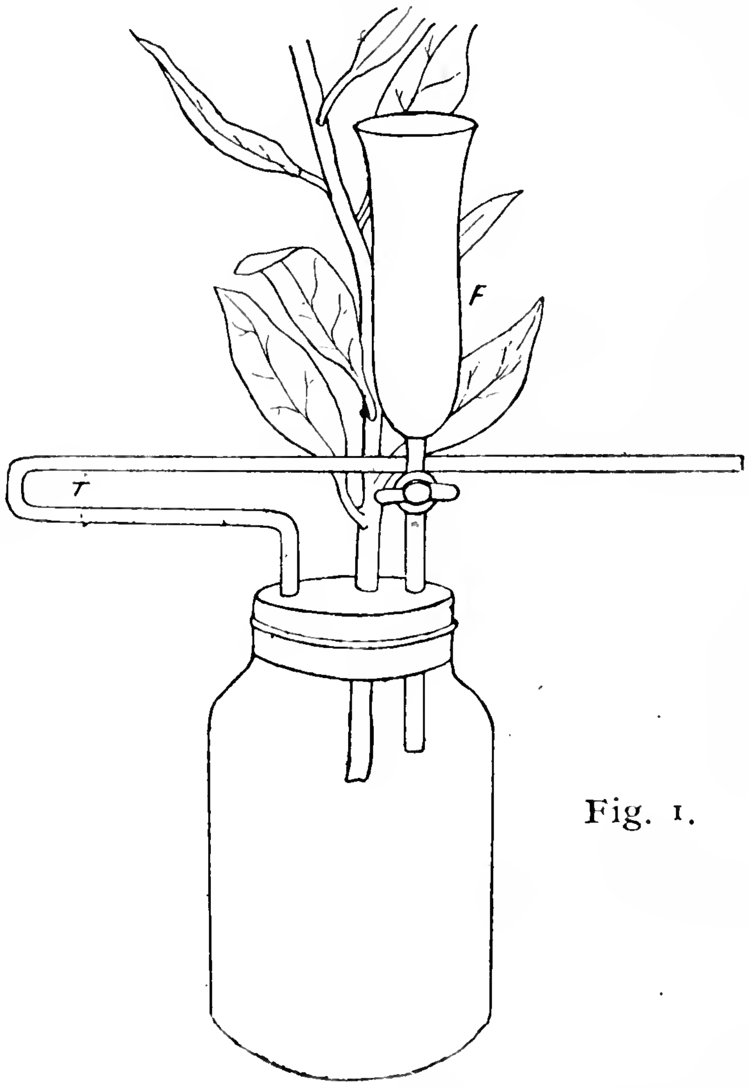


Fig. 1.

neck of the bottle, It should be observed that only woody stems are suitable, as otherwise there is the risk of the tissues being too much compressed to allow of the free passage of tbe transpiration current.

To start the apparatus, after the cork is provided with its proper complement of tubes, funnel and shoot, all that is required is to fill the bottle with water and then to press in the cork. The funnel (which of course must be higher than the horizontal limb of the tube T) is filled with water, and the tap opened so as to allow

water to pass into the bottle. Any air that may be present is driven out through the glass tube, which then fills with water.

The particular advantage of the apparatus lies in the ease with which an experiment may be started. When not in actual use, as the water is transpired of course air follows the column of water into the bottle, but this can at once be ejected by allowing water to to flow from the funnel, and an observation taken without any disturbance of the plant under investigation. It may be added that 20 inches is a convenient length for the upper limb of the glass tube,but of course it can be made as long as may be desirable, at least within the limits of practical rigidity.

J. B. FARMER.

THE DISTRIBUTION OF THE IRISH FLORA.

UP to the present date the flora of Ireland has usually been analysed according to the eight types of distribution, established by H. C. Watson[1] for Great Britain, namely:—

1.	British type	-	species occurring throughout Britain.	
2.	English type	-	,, ,,	in the south of Britain.
3.	Scottish type	-	,, ,, ,,	north of Britain.
4.	Intermediate type		,, ,,	chiefly in Mid-Britain.
5.	Highland type	-	,, ,, ,,	in the mountains.
6.	Germanic type	-	,, ,, ,,	in East England.
7.	Atlantic type	-	,, ,, ,,	in West ,,
8.	Local type, including species occurring in a few localities.			

In the first portion of an extremely interesting paper, Mr. Lloyd Praeger[2] gives an account of the distribution in Ireland of Watson's types. A large number of common plants (377 species) are of purely British type; only eight of those occurring in Britain are absent (*e.g. Avena pratensis*), these being mostly of southern distribution (British-English type). The English type decreases from S.E. to N.W., being most common in Dublin, Wicklow and Wexford, whilst the Scottish type is concentrated in the North and from there extends down the coast on either side. Whereas a considerable percentage of the former type owes its presence in Ireland to the operations of man, the latter is purely native. The abundant occurrence of plants of English type in Clare is curious, and is probably correlated with the presence of limestone surfaces in that county. The Highland type is not very abundantly repre-

[1] Cybele Britannica, I. 43 (1847), iv. 409 (1859), and Compendium of the Cybele Britannica, 23 (1868-70).

[2] Proc. Roy. Irish Acad. Vol. xxiv., Sect. B, Part 1, 1902, pp. 1-60.

sented and its limits by no means correspond with the distribution of highlying ground.

The Germanic type is least abundant of all, which may be accounted for by the breaking down of the Irish-English land-connection before that of the English-Continental; all the thirteen species present are distinctly calcicole. The group attains its maximum in Clare, S.E Galway and Dublin. The Atlantic type is well represented, a considerable number of the species present being maritime and consisting of plants adapted to the conditions of an insular climate; corresponding to this we find that this type is coastal in its distribution, but rather southern, occurring chiefly in South Kerry, West Cork and Waterford.

If the distribution of calcicole and calcifuge plants be considered, it is found that the former are most abundantly represented in the West and not in the central Limestone Plain; they reach their maximum in Clare, S.E Galway and Limerick, occurring rather commonly also in E. Cork, Kilkenny, Kildare and Dublin. Mr. Praeger points out that the occurrence of bare limestone rock accounts for the great development of the calcicole group in the west, whereas the limestone drift covering the rocky surface of the Central Plain and Eastern counties may frequently have all the lime washed out of its surface layers, leaving a non-calcareous soil. The calcifuge plants are more abundant, occurring especially in Kerry and West Cork. They thus reach their maximum on the old non-calcareous rocks grouped round the coast and their minimum in the limestone plain. The county Clare is remarkable in that there both the calcicole and the calcifuge flora are richly developed.

It is noteworthy that the distribution of 'Scottish,' 'Highland' and 'Atlantic' plants is to some extent analagous to that of the calcifuge flora, whereas that of the 'English' and 'Germanic' agrees in many respects with that of the calcicole group; this corresponds well with the petrological conditions prevalent in the areas of Britain occupied by Watson's types.—In Ireland the overlap between northern and southern forms is apparently less marked than in England.

It will be noticed that a natural geographical grouping of Irish plants is not possible with the use of Watson's types, and Mr. Praeger devotes the second half of his paper to the solution of this question. He finds that Irish plants may in the first place be grouped in two classes—those which do and those which do not show an aggregation in some part of the country. The latter are all included under a

"General Type of Distribution" and correspond largely (over 260 species) to the plants of Watson's British Type, although a certain number are British-English, English-British, or belong to others of Watson's types. It will thus be seen that the "Universal" plants of Ireland, which are not so widespread in Great Britain, have a more of less southern range in this latter island, except for *Crepis paludosa*, which is distinctly northern (Scottish-Highland).

Coming now to the plants which show an aggregation or diminution in some part of the country, we first find a marked tendency towards a central or marginal distribution; this feature is not very noticeable in the flora of Great Britain and is due to the position of the non-calcareous rocks and mountain-groups around the edge of Ireland, whilst the central limestone portion is low-lying and possesses numerous bogs, marshes and lakes. It is accordingly possible to establish a "Central Type of Distribution" for Ireland, for plants found chiefly in the central plain; this type has an area extending between a line joining the Shannon with Waterford on the south and another joining Sligo and Dundalk bays on the north.

The plants concentrated around the edge of the island constitute a further "Marginal Type of Distribution," whose most characteristic feature is its avoidance of the central plain. A number of plants of marginal distribution are restricted to limited areas or show a general increase towards north, south, east or west. Thus a line, running east and west and joining Galway and Dundalk bays, marks off the northern from the southern species; and it was found necessary to draw a further boundary line, running north and south through the cities of Londonderry and Cork, to divide the eastern from the western plants. These two intersecting lines define four further types of distribution, named after the four provinces of Ireland, in which each reaches its maximum development. The seven types of distribution, thus defined for Ireland are 1 General (Universal), 2 Central, 3 Marginal, 4 Ultonian, 5 Mumonian, 6 Lagenian, 7 Connacian.

To the Central type 38 species (*e.g. Stellaria palustris, Orchis Morio, Sium latifolium, Andromeda polifolia*) are referred, which are all lowland; of these eleven are aquatic and nine are marsh plants; ten grow on pastures and dry ground, whilst two are bog plants. Further whereas eight are calcicole, none are calcifuge. Compared with their British distribution, the plants of this group are distinctly southern.—46 species (*e.g. Hypericum elodes, Lobelia Dortmanna, Pinguicula lusitanica, Nitella translucens*) are included

in the Marginal type[1], one half of them being characteristic upland species; this type is mainly alpine, calcifuge, or xerophytic, these sections being due to the numerous mountain groups, the absence of limestone and the sands of the coast respectively. Their distribution in Great Britain is very varied.—The Ultonian type includes 45 species (*e.g. Saxifraga oppositifolia, Circaea alpina, Cicuta virosa, Potamogeton filiformis*), about 30 of which are hill or mountain species, both calcicole and calcifuge species being absent. In Great Britain this type is chiefly Highland and Scottish in distribution.—The Mumonian type has 66 species (*e.g. Ranunculus Lenormandi, Pinguicula grandiflora, Campanula Trachelium, Chlora perfoliata*), more than half of them inhabiting pastures, light soils and dry places. They are markedly southern and western in distribution in Great Britain.—49 species (*e.g. Lepidium hirtum, Trifolium glomeratum, Cynoglossum officinale, Scilla verna*) belong to the Lagenian type, which is to a great extent xerophytic in character. Its distribution in Great Britain is chiefly "English."—The Connacian type has 63 species (*e.g. Taxus baccata, Adiantum Capillus-Veneris, Habenaria intacta, Erica mediterranea*) and is chiefly made up of calcicole, mountain and bog-plants. The distribution of the group in Great Britain is quite heterogeneous.

It is interesting that certain plants of wide distribution in Ireland are absent from definite areas; thus *Drosera anglica* is absent from the south-eastern counties alone (Anti-Lagenian type), whereas *Oenanthe Phellandrium* dies out along the mountainous edge of the island. These plants are best included in smaller types of distribution and termed according to their most conspicuous feature "Anti-Ultonian," "Anti-Central," etc.

The aliens were generally found to possess a discontinuous range, a large number being widely distributed, whilst others fall in with various types of distribution. These latter are chiefly aggregated in the south and east of the island; Mr. Praeger accounts for this in the following words: "The great Leinster anticline is an important factor in Irish plant distribution, and a phytological boundary of marked character is formed by the line where its uplands sink into the Central Plain, and by the prolongation of that line northwards and southwards."

Very little can as yet be said as to the causes which have led to the present distribution of the Irish flora. The effect produced by the nature of the soil is sufficiently obvious, but with regard to

[1] Maritime plants, which are generally distributed round the coast, are considered to belong to the General Type.

climatic conditions the subject is not so clear. Some of the characteristic members of the Connacian group are, however, undoubtedly frigofuge and their distribution is corresponding. Further parallels between isophytic and isothermal lines may be drawn without difficulty amongst the southern and western plants. Nevertheless much information is still wanting before we can determine how far the present distribution of the flora has been effected by conditions of climate.

THE PODOSTEMACEAE OF INDIA AND CEYLON.

It is no easy matter to elucidate the extremely complex morphology of an order like the Podostemaceae and botanical science is indebted to Mr. Willis, for a valuable contribution towards the knowledge of this interesting group of aquatic plants,[1] which is so completely adapted to a life in rushing water. In fact the habitat of the Podostemaceae is so unique, that their only competitors are a few specialised Bryophytes: and since the different genera are adapted to water of different speed there is even little struggle for existence amongst the various members of the order. Such a state of affairs has allowed of an extreme of morphological differentiation only paralleled elsewhere in the vegetable kingdom amongst the seaweeds, whose external morphology is frequently copied to a considerable extent in the vegetative organs of the order in question.

Except in the concluding remarks, Mr. Willis's paper deals only with the Podostemaceae of India and Ceylon, and the forms there represented are amongst the most specialised of the order. This specialisation, which evinces itself in the more or less extreme dorsiventrality and flattening of the horizontal portion and reduction in size of the secondary shoots of the plants in question, is regarded more as an adaptation to the dangers of a life in flowing water, than to the rapid current itself. Plants, such as the Podostemaceae, which live in a rapidly-flowing stream, are continually exposed to the danger of a fall of the water-level and are also probably subjected to a considerable scour. Mr. Willis points out that many of the South American Podostemaceae, which have well-developed leafy shoots, live in very swift water, so that

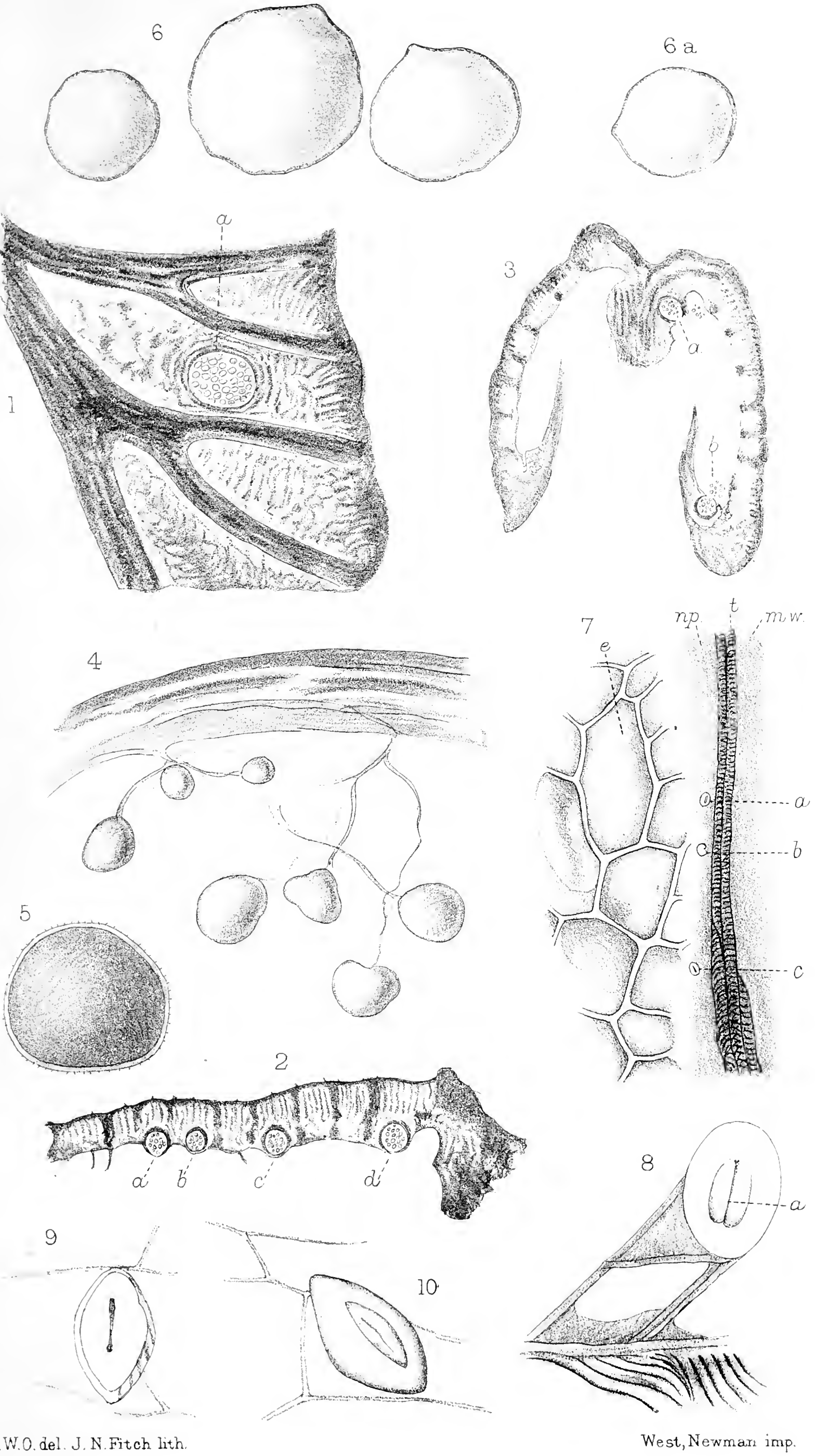
[1] J. C. Willis. Studies in the Morphology and Ecology of the Podostemaceae of Ceylon and India. Annals of the Royal Botanic Gardens, Peradeniya. Vol. I., part 4. September 1902. (Plates iv.—xxxviii.)

this latter factor in itself would not appear to be the cause of the specialisation in external morphology, attained by the Indian members of the order. There seems, however, no reason for assuming that it has played no part in the evolution of the plants in question.

In general the plant in the Podostemaceae may be said to consist of a horizontal portion, which is in more or less intimate contact with the substratum and from which numerous secondary shoots are endogenously formed. This horizontal part is apparently of root-nature (except in *Lawia*), but it is preferable not to denominate it root, as most of the structures concerned would scarcely come under our ordinary conception of this organ. The term *thallus*, which Mr. Willis proposes, seems quite useful in this connection. In most cases the growing-point of this thallus has a distinct collenchymatous cap; the branching is either endogenous or exogenous. Starting with *Tristicha ramosissima*, which inhabits relatively slow-flowing water and has a purely filamentous thallus, a whole series of stages may be found ending in the broad, flattened liverwort-or lichen-like structures of the *Hydrobryums* of the rapids.

The thallus buds out laterally (and generally endogenously) from the primary axis which is developed from the germinating seed. The embryo is always destitute of a radicle and the hypocotyl immediately bends towards the substratum, to which it becomes attached by rhizoids and frequently also by the haptera, so characteristic of the order. In general the primary axis remains quite short, only four or five leaves beyond the cotyledons being developed; In *Hydrobryum olivaceum* however it may attain a height of as much as 5 cm., and bears a number of long leaves at its apex, whilst certain very much elongated shoots, found in connection with the adult thallus and secondary shoots of *Willisia selaginoides*, have been interpreted by Mr. Willis as the primary shoots of this plant. Such cases lead to the assumption that the Podostemaceae have arisen from ancestors with well-developed primary shoots, from which lateral adventitious roots arose.

It is impossible in the limited space I have at my disposal, to give any conception of the variety of form that can be assumed by the mature thallus, and I will only mention that in some species of *Dicraea* and *Hydrobryum* considerable polymorphism of this organ of the plant prevails. The numerous secondary shoots, which arise from the thallus, also differ greatly in character in certain genera. In *Tristicha* and *Podostemon* they are well developed, whilst in the



F.W.O. del. J. N. Fitch lith. West, Newman imp.

majority of the Indian Podostemaceae they are much more reduced and bear small, sheathing leaves. The shoots of *Tristicha* are peculiar in that they develop numerous further shoots of the second order (ramuli). These latter are of limited growth, and bear smaller leaves than the main shoots. In the angle between these latter and the ramuli buds arise, many of which develop into shoots of unlimited growth, which repeat the structure of the main axis. Others of these buds, however, remain dormant till the flowering period, and then develop into floral shoots. In the other genera we observe a reduction in size of the secondary shoots, which goes hand-in-hand with the increasing dorsiventrality of the thallus; at the same time the secondary shoots may themseves show a very marked dorsiventral structure. In *Willisia selaginoides* it is note-worthy that these shoots attain a considerable height (2—7 cm.) and stand stiffly out into the water, a strong band of lignified tissue around the central strand, enabling them to resist the force of the current.

At the end of the rainy season, when the water begins to fall, the flowers are developed and by the time they get exposed to the air, they are ready to open. In all the flattened forms they are developed terminally on a secondary shoot, a number of the leaves being transformed into bracts by the falling away of their upper portions and an increased development of the base. In *Lawia* they are borne on special shoots, which arise from one of the many marginal growing points of the flattened thallus. In *Tristicha* their development on branches of the main secondary shoots has already been mentioned; in this genus they are only rarely found on secondary shoots, arising directly from the thallus. The anemophilous flowers are generally destitute of a perianth (excepting *Tristicha* and *Lawia*), its place being taken by a closed spathe, which protects the young flower. In *Farmeria* and *Hydrobryum sessile* the flower is sessile, but it is usually provided with a short peduncle, which elongates considerably later on; after the flowering is over the inner part of the cortex of the peduncle becomes thick-walled and strongly lignified and the outer thin-walled portion falls away entirely, leaving the ripe fruit standing on a much thinner pedicel than before and on a highly elastic one, which is probably of advantage in the dissemination of the seeds. Another interesting adaptation is observed in some of the flattened forms at the time of flowering. In these only a certain number (generally about one-third) of the secondary shoots ultimately become

floriferous; the vascular tissue, leading to them, which up to that elements and the surrounding cortical tissue becomes thick-walled, time is as usual totally undifferentiated, now develops typical xlyem whilst the remaining unaltered portions of the thallus soon wither or fall away entirely. By the development of these conducting elements, the floral shoots, which are no longer submerged at the time of flowering, are supplied with the necessary food-materials and moisture.

One of the most important points, brought out by Mr. Willis's paper, is the gradual transition from radial to dorsiventral floral structure, which can be observed in the Podostemaceae, and which can scarcely be accounted for on the principle of natural selection. The flowers of *Tristicha ramosissima* show radial symmetry, but in the other genera, in which the thallus exhibits such a marked dorsiventral structure, this also becomes more and more apparent in the floral organs, just as it does in the secondary shoots. This dorsiventrality of the flower evinces itself first in the suppression of certain of the floral organs and leads up to the extremely dorsiventral flower of *Farmeria metzgerioides*, in which one of the two loculi of the ovary is much more strongly developed than the other, which is practically abortive. If anything this zygomorphism of the flower is a positive disadvantage, and cannot be regarded as having arisen as an adaptation to the mode of life. Mr. Willis considers it to be the result of correlation in relation to the vegetative organs, and thinks that the dorsiventrality of the flowers has been forced upon them by the dorsiventrality of the former. It is at least remarkable, that the more flattened and dorsiventral the vegetative organs are, the greater is the degree of zygomorphism evident in the flower. *Lawia* forms an exception to this rule, in that, although the vegetative organs exhibit an extreme of dorsiventrality, the flower itself is radially symmetrical in structure.

The author also extends this view of the origin of dorsiventrality in the flower of the Podostemaceae to the zygomorphic floral structure of the other orders and points out that correlation may in many cases have done more towards determining the structure of an organ than natural selection.

F. E. FRITSCH.

CELAKOVSKY ON THE CORTICATION OF THE STEM BY FOLIAR BASES.[1]

HOFMEISTER first shewed that in the majority of leafy plants the outer cortex of the stem was formed by the decurrent bases of the leaves. Celakovsky further elaborates this by shewing firstly that in all cases where at the apex of the stem the leaf-rudiments are in complete contact with each other any two superposed leaf-rudiments are separated, as seen in longitudinal section, by a perfectly acute angle, the apex of which is on the axis. As, therefore, a mathematical line divides the insertion of both leaf-bases, no free portion of the axis can possibly exist in that region. It follows that the internode formed at a later stage between the two leaves thus in complete contact with one another can only arise by means of an extension of *the base of the upper leaf* taking place simultaneously with that of the axis on which it is inserted.

But cases occur in which the leaf-rudiments are, from the earliest stage, separated from each other by conspicuous areas of the central axis. These spaces constitute the "Entwickelungsfelde" of the Schwendener-theory, the arena of the development of the young leaf which is gradually wholly occupied by the latter as it grows, both in breadth and thickness, more quickly than the axis itself, expands in the tangential and the radial directions respectively. This primary more rapid *growth in thickness* of the leaf-rudiment, which enables it to occupy the *axial* space intervening between itself and the leaf-rudiment immediately below, must not be confused (as was done by Hofmeister) with the subsequent extension of its base on formation of the internode. Further, this latter process involves a restitution to the axis of that which was originally taken from it. For the cortical tissue of the internode, although in its origin arising from the leaf ("Blattbürtig") must be regarded as pertaining to the stem ("Stammeigen.") This reciprocity in growth between the leaf and the subjoined stem-segment ("Stengelglied") is an indication of the morphological unity of the two, and of the fact that they together constitute what our author terms the ("Sprossglied.")[2]

Celakovsky then proceeds to describe typical examples taken

[1] "Die Berindung des Stengels durch die Blattbasen,," Flora, Heft, III., 1902.

[1] See his "Die Gliederug der Kaulome" (Bot. Zeit. 1901), or my review of the same (New Phytologist, vol. I., January, 1902).

from the various groups of plants, of the process of cortication of the stem by means of leaves. Among the Phycophytes *Chara* exhibits a striking illustration of the phenomenon. As do also the Mosses among the Bryophytes; yet in *Chara coronata* and *C. stelligera* and all *Nitellas* axial internodes are present from the earliest stage onwards, and no cortication is possible. Of the Pteridophytes excellent examples are afforded by *Equisetum* and *Selaginella*. But perhaps the most remarkable and at the same time familiar instance of the phenomenon is revealed by the Coniferae; one section, however, the Abietineae differs from the rest in the fact that the foliar base ("Blattkissen") here has a mixed origin, *its lower portion arising from the axis*, and its upper, broader portion from the leaf base; the former is already present at an early stage of the young bud, the latter is first formed on elongations of the axis. As regards the Phanerogams several cases, both from the literature and our author's own observations, are cited, in which the apical buds exhibit complete contact between the young-leaf rudiments and subsequent cortication of the stem by the extension of their bases.

Finally, he points out that further investigations are needed in order to shew whether there may not be cases in which, as in some Charas and the Nitellas, contact between the young bases, and cortication by the early-formed stem-segments ("Stengelglieder") do not occur. For this purpose plants like the Cactaceae, possessing rudimentary foliar organs are recommended.

W.C.W.

THE LONDON BOTANICAL SOCIETY.

THE February Meeting of this Society was held in the Biological lecture-room, Royal College of Science, on Monday, 16th ult.

The Secretary, Professor Farmer, shewed an interesting series of lantern-slides from photographs taken by himself in the autumn of 1902, illustrating the vegetation of certain districts of Ontario, Canada. Several were of the litoral flora of Lake Ontario. One of the most striking shewed magnificent plants of the common silverweed (*Potentilla anserina*) binding the loose sand of the lake shore.

Dr. F. E. Fritsch read a paper on "Recent Discoveries of Caoutchouc in Plants." Most of the substance appeared in the last number of the New Phytologist (Vol. II., No. 2, pp. 25-30). The possible

phylogenetic importance of the type of laticiferous element found in *Evonymus* and certain Hippocrateaceae was treated in greater detail, and a table was drawn up to show how the type of laticiferous element found in Euphorbiaceae, Apocynaceae, etc , on the one hand, and the articulated latex-vessels (Cichoriaceae, Papaveraceae, etc.) on the other, might both have been derived from the elements in question. Dr. D. H. Scott, Professor Farmer, Mr. W. C. Worsdell and Mr. A. G. Tansley took part in the ensuing discussion, which was chiefly devoted to the mode of development of laticiferous tissue in general.

CORRESPONDENCE.

To the Editor of The New Phytologist.

Dear Sir,

Will you allow me through the medium of your paper to call the attention of those who publish lengthy accounts of important researches, to the immense benefit they always confer upon students and others by collecting the chief results of their investigations in the form of a summary at the end of the account.

Though intricate details and columns of figures may be of the greatest use to the specialist, the student reading for an examination has usually neither the time nor the inclination to wade through them, while at the same time it is important for him to keep well informed about any new facts which they have brought to light.

Moreover, a research is but half completed, when the investigator omits to draw conclusions from his results and neglects to consider what bearing they have upon the present knowledge of the subject.

Yours faithfully,

Christ's College, Cambridge, A.W.B.
8th, Feb. 1903.

OBITUARY.

ALFRED VAUGHAN JENNINGS, F.L.S., F.G.S., who died on January 12th last, at Christiania, was the son of the Rev. Nathaniel Jennings of Hampstead. He was educated at St. Paul's School and afterwards at the Royal College of Science, South Kensington, where he was a student underHuxley and was *proxime accessit* for the Forbes Medal.

At the close of his collegiate career Mr. Jennings obtained an appointment in the Geological Department of the College and soon afterwards became also teacher of Biology to the Evening Classes at the Birkbeck Institution. Mr. Jennings proved a very able teacher, and into the Evening Classes he threw more energy than his health would permit. Nevertheless, he and his colleague in Botany, Mr. David Houston, F.L.S, attracted a large and enthusiastic body of students and they laid the foundation of the present school of Biology at this Institution.

Later Mr. Jenning's health broke down and he was obliged to take a voyage to New Zealand. On his return he held a post for a short time in the Royal College of Science, Dublin.

Mr. Jennings was an omnivorous and untiring Collector in Zoology, Botany and Geology, and was the author of several original papers in each of these three branches of Natural Science. The illustrations to his papers and his drawings in the Whitechapel Museum show that he possessed considerable artistic ability.

In disposition Mr. Jennings was modest and retiring and very kindly and generous. No student ever came to him for help and was refused.

Had Mr. Jennings' very brilliant brain been supported by proportionate bodily health, he would have achieved much, possibly as much as he was always hoping to be able to accomplish.

For the last ten years his existence had been but a fight for life, and his best friends can only be thankful that this fight is now ended. K. M. H.

THE ORIGIN OF THE PERIANTH IN SEED-PLANTS.

IN the February number of the New Phytologist, Mr. Worsdell gives a brief resumé of various facts and theories bearing on the origin of the perianth in Angiosperms with special reference to Celakovsky's views as illustrated by the Natural Order Ranunculaceae.

At the outset the writer expresses the opinion "that fertile foliar organs (or sporophylls) preceded in time all other kinds of leaves, and that the latter have been gradually differentiated from the former by a process of sterilisation of their tissues." This however need not imply the derivation of the perianth from sporophylls in the highest group of plants. The differentiation of foliage leaf and sporophyll was an established fact before the

evolution of the angiosperm, and there is therefore no *apriori* reason for deriving the floral envelopes in the latter group from sporophylls.

The writer concludes with the statement "that everywhere both calyx and corolla, may lay claim to a similar place of birth, *viz:* in the andrœcium, however distinct or dissimilar from each other in almost every character they may at times appear."

It is difficult to accept this statement in its entirety. The flowers which we are inclined to regard as the most primitive are unisexual and have presumably not been derived from an hermaphrodite type; yet we find in the female, as well as in the male, instances of a well defined perianth, which in the case of the female could not have originated from an andrœcium. Hence the origin of perianth from andrœcium cannot have been universal.

It may be of interest to note the relation which the perianth bears to the sporophylls in some of these "early" simple-flowered orders.

Salicaceae comprises the two genera *Populus* and *Salix*. In the poplars, which are wind pollinated, we find in both sexes a cup development of the axis below the sporophylls. This cup is the first developed part of the flower; its position and development suggest a simple perianth, and there is no reason for associating its origin with either stamens or carpels; it is an outgrowth of the floral axis preceding the sporophylls in time and space. In *Salix*, where entomophily has arisen, we find in a similar position one or two small honey-secreting glands. If these are homologous with the cup in *Populus*, they are in comparison much reduced and late in development. Their degree of development shows considerable variations, and in many species the reduction is more complete in the female flower than in the male. Thus, while in the male of many species a posterior and anterior gland is present, the anterior is absent in the female. In some cases the glands are united laterally below to form an inconspicuous lobed hypogynous ring (as in *Salix tetrasperma*).

We may compare this reduction of the perianth in *Populus* to a nectary or nectaries in *Salix* with the similar reduction of petal to nectary in Ranunculaceae, and associate it with the entomophily of the latter genus. The occasional appearance of hermaphrodite flowers in the willow has suggested the derivation of the unisexual flowers from an hermaphrodite -type, but the argument may be used in the other direction and the hermaphrodite flower be regarded as

the later development. If however we imagine the typical *Salix* flowers to be derived from an hermaphrodite type we should not expect to find the glands, on the view that they represent a perianth derived from the andrœcium, more numerous in the male than in the female.

Betulaceae comprises the two tribes Coryleae and Betuleae. In Coryleae *(Corylus, Carpinus)* the male flower has no perianth; it stands in the axil of a bract and consists of four stamens preceded by two bracteoles. In the female flower there are however in addition varying numbers of epigynous scales (*i.e.*: a rudimentary perianth). There is no suggestion that these perianth scales in the female flower represent the lost stamens of an hermaphrodite flower.

In the other tribe Betuleae the state of affairs is reversed. In one section (Gymnothyrsus) of *Alnus* the male flower has a four-leaved gamophyllous perianth, and the four stamens are opposite the perianth leaves. In other species of *Alnus* (§ Alnaster and § Clethropsis) and in *Betula* the perianth leaves are free and fewer in number, often only two. In the female flower there is no perianth. If the unisexual flowers had a common origin from a hermaphrodite type we might expect a similarity of arrangement in the two sexes.

A comparison of the male flowers in the two tribes is suggestive. In Coryleae where there is no perianth the stamens are well protected by the bract and bracteoles; in *Alnus* a similar protection is afforded by the four perianth leaves, which are placed immediately behind each stamen; there is no reduction in the number of stamens. In *Betula* where there are only two (median) stamens, often only the two median perianth leaves are developed. Associated with this development of perianth in Betuleae is a partial (*Alnus*) or complete (*Betula*) suppression of the bracteoles of the two lateral flowers of the dichasium.

The suggestion is that the perianth is protective; it is however not easy to associate it directly with the suppressed bracteoles, as its development is the same in all three flowers of the dichasium, whereas the bracteoles of the central flowers are both present. In the female flowers of the Coryleae where the bracteoles are present and help to form the involucre, the perianth consists of, as far as we can see, functionless outgrowths. If it is not possible to regard the perianth as a new foliar outgrowth *sui generis*, we must seek its origin in additional bracteoles which in the male flowers have

been made use of, while in the female they are apparently still useless structures.

In Fagaceae the perianth is an established fact. In the male flower, according to Prantl, the stamens correspond in number, and stand before the 4 to 7 basally united leaves of the perianth, or are present in an increased (to double) number. In *Nothofagus obliqua* both stamens and perianth segments are numerous (30-40). In the female there are generally three carpels and a six-leaved (3 + 3) superior perianth. Here both in male and female we note the elaboration of the perianth into two regularly alternating series. The flowers are invariably monoecious, and generally diclinous, in *Castania* and *Pasania* the catkins are androgynous and hermaphrodite flowers may occur at the limits, between the male and female portions of the inflorescence. A "rudimentary pistil" in the form of a hairy hump is also present in the male flowers in these two genera, and the same may be indicated by thread-like structures which are sometimes present in the same position in *Quercus* and *Pasania*. But even if we are inclined to assume that the flowers generally are derived from an hermaphrodite type there seems no suggestion of the derivation of the perianth from the andrœcium. In the male flower the numbers in the two series, perianth and andrœcium, vary in the same direction, an increase in the number of perianth leaves is associated with an increase, not with a decrease, in the number of the stamens. Bracts and bracteoles are present and there is besides, if we regard the cupular structures as of foliar origin, a remarkable development of additional bracteoles around the female inflorescence or flower.

In his recently published monograph[1] of the Myricaceae M. Chevalier indicates several points of interest in the development of the male and female flowers. The inflorescence may be a simple catkin, or the catkin may be more or less branched. Androgynous catkins occur and hermaphrodite flowers have been recorded. There is no perianth, but the function often associated with a perianth may be performed by the bracteoles. The bracteoles arise as a pair of outgrowths on the floral axis, and recall in their form and structure the bracts in the axil of which the flower arises, but are more reduced. The number of stamens is variable; the bracteoles, arise as outgrowths "similar to those which produce the stamens and belonging to the same cycle," they are placed right and left of the flower and with the bract constitute a protective arrange-

[1] Mémoires de la Société Nationale des Sciences Naturelles, &c., de Cherbourg, vol. xxxii.

ment. In the female the terminal bicarpellary pistil is at its first appearance flanked right and left by a small outgrowth, the bracteole rudiment. The degree of development of the bracteoles varies in the three genera (*Gale*, *Comptonia* and *Myrica*), and affords one of the best characters for generic diagnosis. They form, in brief, a cupular perianth-like structure which in *Gale* and *Comptonia* are agents for distributing the fruit. The association of these bracteoles with the sporophylls both in origin and position is so close that they might as well be regarded as a perianth. Presumably they are homologous structures in the two sexes, and there is no reason to suppose that the unisexual flowers are reduced from an hermaphrodite type, and therefore no reason to derive them from stamens. Their development suggests that they are foliar outgrowths below the sporophylls variously elaborated in the three genera and the flowers of the two sexes for protective and seed-distributing functions.

In Juglandaceae the relationship between perianth and bracteole is very close. A rudimentary pistil is sometimes present in the male flower and it has been suggested that the general unisexual condition has arisen by reduction of hermaphrodite flowers. The male flower of *Platycarya* consists of 8-10 stamens in the axil of a bract, there is no trace of a perianth, but in the female flower the pair of bracteoles are united with the sides of the ovary suggesting an epigynous perianth. Similarly in *Carya* the male flower is naked, but in the female there is a single posterior perianth leaf which like the bract and the lateral pair of bracteoles is united with the ovary the four leaves simulating a 4-partite perianth. *Engelhardtia*, *Pterocarya* and *Juglans* have a generally 4-partite perianth in flowers of both sexes. In the male the floral axis is elongated in the direction of the subtending bract along which bracteoles and perianth leaves are arranged below the stamens; the perianth leaves bear a strong resemblance to the bracteoles with which they share the protection of the stamens, but are generally smaller. In the female flowers of *Engelhardtia* and *Pterocarya* the perianth is epigynous, while in *Juglans* the bracteoles are united with the ovary and form a toothed ring below the perianth. There is a strong suggestion of homology of perianth and bracteoles, and it is difficult to imagine a different origin for the two sets of leaves. It is of course possible, assumiug the derivation of the flowers from an hermaphrodite type, to regard perianth and bracteoles alike as barren sporophylls.

In Saururaceae and Piperaceae both bracteoles and perianth are absent. The flowers are simple and hermaphrodite or unisexual, presumably by abortion; the abortion of the stamens which also occurs to some extent in the hermaphrodite flowers (compare *Houttuynia* and *Saururus*) never results in the formation of a perianth. The bract which subtends the flower is more or less developed as a protective structure often encircling the base of the stamens and ovary, and this may be associated, as in *Piper nigrum*, with a concavity of the thick axis of the spike in which the flower is partially immersed. In Chloranthaceae also the flowers are hermaphrodite or unisexual. In *Chloranthus* the hermaphrodite flower stands in the axil of a bract, there are no lateral bracteoles, but a small scale structure ("perianth") arises at the base of the ovary in front of the bract; the flower is gynandrous.

The single central stamen of the male flower of *Casuarina* has a pair of bracteole-like perianth leaves which occupy the median position, alternating with the two lateral bracteoles; the anterior perianth leaf may be absent. In the female the lateral bracteoles are present but no perianth leaves.

In typically monochlamydeous flowers with a single whorl of stamens, such as occur in Ulmaceae, Moraceae or Urticaceae, the perianth leaves are opposite the stamens. This suggests rather a protective foliar outgrowth of the floral axis than a modification of a lower whorl of sporophylls.

Turning to Monocotyledons we find in *Najas* the single axial stamen of the male flower, surrounded by a sac-like protective outgrowth developed below it; we may call this a perianth. A second similar and lower outgrowth (the spathe) which is also sometimes present in the female flowers, may be compared with the bract or spathe which surrounds the cluster of female flowers in *Zannichellia* and is so frequently associated with the the flowers of submerged monocotyledons belonging to the Helobieae series.

Other examples might be adduced which indicate that the origin of the perianth is not invariably to be sought in the modification of the members of the andrœcium.

In many of the cases which we have quoted there is a strong indication of homology between bracteoles and perianth leaves. There is also a suggestion that the simple perianth originated from foliar outgrowths of the axis below the sporophylls, for the protection of the sporophylls.

An order like Ranunculaceae, though with relatively simple

flowers, shows a further elaboration of the perianth into two distinct series, an outer (calyx) for protection, an inner (corolla) for attractive purposes. Frequently the inner is more or less reduced to nectar-containing structures when the attractive function is performed by the calyx. Mr. Worsdell puts forward Celakovsky's view that the petaloid calyx represents a more primitive form than the green calyx of other members of the order and of most Dicotyledons. It is not easy to correlate this with the view that the earliest flowers were wind fertilised, and that a petaloid development occurred later as an accompaniment of entomophily. The protective calyx of the dichlamydeous flower, seems comparable rather with the simple protective perianth of the monochlamydeous flower, while the corolla is a later development and in many cases may have arisen by modification of stamens. The stamens are often highly attractive without showing any structural modification; in *Potamogeton* a petal-like structure grows out from the back of each stamen; generally however the sporogenous character becomes lost in the conversion of stamen to petal.

Too much stress should not be laid on the interchangeability of function in various Ranunculaceae to which Mr. Worsdell refers. Where a floral axis bears bracteoles, sepals, petals, stamens and carpels following in a more or less continous spiral, it is not a matter for surprise, that, with a number of foliar organs arising thus in simple succession on the same axis, there should be an absence of definiteness in the limitation of distinct series.

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THE SEED OF *LYGINODENDRON*.

THE communication made to the Royal Society on May 7th by Professor Oliver and Dr. Scott contained the most important discovery bearing on the great problem of the connexion of the Flowering with the Flowerless plants which has been made since Hirase in 1896 found motile antherozoids in the pollen-tubes of *Ginkgo*. Hirase's discovery, supplemented by those of Ikeno in *Cycas* and of Webber in *Zamia*, shewed that a character which had previously been thought to be confined to the Pteridophytes had been retained in a few of the Gymnosperms, and thus so to speak, pulled up a thread from below to bridge the gulf between the two classes. Oliver and Scott have now shewn that a coal-measure plant of fern-like habit and largely fern-like anatomy produced a structure which in most of its essential features must be called a seed, and have thus pulled down a thread from above to bridge the same gulf. When we consider, indeed, the extremely complete series of forms (making up Potonié's group the Cycadofilices) which lead up from a typical fern-structure to typical Gymnosperm-structure in the details of vascular anatomy, and when we add to this the two discoveries which have just been alluded to, it becomes very doubtful whether we should any longer speak of a "gulf" between the Ferns and the Flowering Plants. Such an excellent bridge is being bit by bit erected, or to vary and perhaps improve the metaphor, the strait of water between the two land masses—a division at one time thought to be the most important in the plant-kingdom—is being so largely filled up with solid earth, that it is already nothing like so important, for instance, as that between the Bryophytes and Pteridophytes, or even as that separating the Bryophytes from the Algæ.

The essential point of the present communication is the conclusion that the coal-measure seed *Lagenostoma Lomaxi* Williamson (MS), a seed with many of the essential features of a modern Gymnosperm, but of considerably more complicated structure, was

borne by the Cycadofilix *Lyginodendron Oldhamium*, a plant of arboreal or semi-arboreal habit, standing far back in the series of forms which connect the modern Cycads with the great Fern-stock. The seed has not been found in actual connexion with the plant—indeed it appears that a layer of separation was formed at its base which caused it to fall off at a comparatively early period—but the two are constantly in association, and what may be called the circumstantial evidence of organic connexion is as nearly conclusive as such evidence is ever likely to be.

The most important part of this evidence is the occurrence, on the peculiar cupule which invests the young seed, of glands which are absolutely identical in structure and dimensions with the glands found on the vegetative organs of *Lyginodendron Oldhamium*, particularly on that form of this plant which is associated with the *Lagenostoma*. These glands are sometimes practically sessile, sometimes shortly stalked, and sometimes capitate with long stalks. All three types of structure, corresponding in every detail, are found both on the cupule of the seed, and on the vegetative organs. There is no other known coal-measure fossil in these much-investigated beds that has glands in the least like the ones in question.

The second piece of evidence is drawn from a young seed to which the pedicel is still attached, and which was evidently detached from the plant accidently before the layer of separation became effective. There is a large vascular bundle in this pedicel, and its structure agrees closely with that of a petiolar bundle of *Lyginodendron*, down to the minute characters of the tracheids.

It will, we think, be generally agreed that we can scarcely refuse assent to the conclusion of the authors that the seed *Lagenostoma* belonged to the plant *Lyginodendron.*

The bearings of the discovery upon the question of the evolution of seed-bearing plants are of the greatest interest. As Dr. Scott remarked in the course of the discussion, it was scarcely to be expected that a plant so low down in the connecting series as *Lyginodendron* undoubtedly is (though its stem and root are largely Cycadean, the whole of the leaf-structure is entirely of Filicinean type), would bear not only a seed-like structure, but such a complicated seed-like structure as *Lagenostoma*. Into the details of this complexity we need not enter here, but they present features which are not found in modern Gymnosperms or in fossil seeds which undoubtedly belong to plants of similar type. It is sufficiently striking that a seed-like structure with a well-marked micropyle and pollen-chamber should

have been borne by such a fern-like plant, but we may perhaps still be permitted to doubt whether *Lagenostoma* was certainly a true "seed" or whether it may not have belonged to a more primitive class of "Protosperms" which had evolved some but not all the characters of true seeds. This of course is partly a question of definition. The two essential points distinguishing a seed such as we find in modern Gymnosperms, from the megasporangium of existing heterosporous Pteridophytes, are, we take it, on the one hand the existence of a pollen-chamber or micropyle, or both, correlated with the germination of the microspore on the megasporangium and the habit of partial or complete siphonogamy, and, on the other, the formation of the embryo completely enclosed in the megaspore (embryo-sac), while still on the parent plant, and the subsequent "germination" of the seed after a resting stage by the growing out of this embryo into the new sporophyte generation.

The first of these features exists not only in *Lagenostoma* but apparently also in *Lepidocarpon*[1] and *Miadesmia*[2] among the Lycopodineæ, while there is apparently no evidence that *Lagenostoma* exhibited the second. This point is not discussed by our authors in the present communication, but no doubt it will be fully dealt with in their larger paper. In general structure, of course, *Lagenostoma* is very much closer to the Gymnosperm type than it is to such structures as the integumented sporangium of *Lepidocarpon* or *Miadesmia*, and this may incline Messrs. Oliver and Scott to the view that the embryo was formed completely within the megaspore and that germination occurred much as in modern Gymnosperms; but the seed certainly fell off the plant at an early stage, presumably before fertilisation had occurred, and of its subsequent history nothing is known. In this connexion it is of interest to note that there is some evidence pointing to relatively late and continuous development of the embryo in Cycads, without the intervention of the definite resting period so characteristic of the higher Gymnosperms and of the Angiosperms, and it is stated that the seed of *Ginkgo* often falls to the ground before fertilization. This type of development of the young sporophyte may perhaps have been characteristic of the primitive Siphonogams.

However this may turn out, it may now be taken as almost beyond question, from the general resemblance of *Lagenostoma* to

[1] See Scott, PHIL. TRANS., 1901; and NEW PHYTOLOGIST, Vol. I., No. 2, Feb. 1902.

[2] Miss Benson, NEW PHYTOLOGIST, Vol. I., No. 3, p.58, March 1902.

the Gymnosperm seed, that the Gymnosperms, or at least the Cycads and their allies, arose from a Fern-stock, and the anatomical evidence on which this conclusion so long solely rested thus receives the most striking confirmation ; while the morphological method in anatomy obtains in its turn a most important justification.

It is with even greater interest that we now await the discovery of more primitive types of seeds in the Filicinean group.

A. G. T.

THE MEETING OF THE "ASSOCIATION INTERNATIONALE DES BOTANISTES" AT LEIDEN.

IT is now about two years since the first steps were taken to establish an International Association of Botanists, the aim of which was (and is) to include in its members all the botanists of the world. The first great object of this Society was to publish an international botanical journal, which should contain abstracts of all important contributions to botanical science, and at the same time give as complete lists as possible of all current botanical literature. The arrangements for this were concluded with the establishment of the "Association Internationale des Botanistes" at Geneva in August, 1901, and the purchase of the "Botanisches Centralblatt," to be conducted as the organ of the Association.

But the publication of such a journal was not the only aim of the Society. Being international, one of its chief objects is to facilitate inter-communication between investigators in the various countries of the world, and a scheme was propounded for the interchange and ready distribution of material for research, as well as for the supply of information on all points connected with botany and botanical travel. This scheme is now slowly maturing, and will, it is hoped, soon be realised,

The difficulties which confront the editorial body of the "Centralblatt" are very great, but slowly and surely they are being overcome. The lists of current literature, for instance, now contain the titles of very recently published papers, and the staffs of special editors, who, in each country, look after the different branches of botany, are now practically complete. This was the essence of Dr. Lotsy's report to the members of the Association at the first gathering of the Leiden conference on the evening of the 14th of

April last. The most important discussions took place on the two following days, and were chiefly concerned with a number of topics, the most important of which will now be dealt with.

Publication of Diagnoses of New Species.

At the meeting of the Association on the morning of the 15th of April, a scheme for the publication of diagnoses of all new species was discussed and approved. These diagnoses are to be published quite independently of the "Centralbratt," will be in Latin and printed on one side of the paper only.

Though the finances of the Association are at present in a fairly flourishing condition, it would not be possible to inaugurate this undertaking unless a sufficient number of subscribers be forthcoming. It is scarcely necessary to comment on the advantage of such a publication to every systematist, the less so, as it is intended to publish the diagnoses of species belonging to the different groups of the vegetative kingdom separately—since diagnoses of species of Musci, for example, are of little interest to a Phanerogamic systematist.

The Central Bureau.

The objects of the Central Bureau are extremely various.

In the first place it is intended to serve as a centre for the supply and exchange of botanical material of every description. Thus for instance various members of the Association have already promised to provide material to which they have special access, and all such material will be supplied to any member desiring it at a minimum cost.

A second object is to form a collection of separate copies of botanical papers, which will be lent to members who may wish to consult them. The nucleus of such a library is already in process of formation by the Secretary.

Another aim is to furnish detailed information to botanists deciding to travel in various parts of the World, concerning such points as routes, climate, cost of living, and possibilities of botanical research.

In order to ascertain the possibilities of furthering these various objects, circulars were sent round some little time ago to all the members of the Association containing questions on such points as those mentioned, and much valuable information has already been obtained in this way. There can be no doubt that with a certain amount of co-operation an organisation of this kind could be easily established.

It is evident that such a Central Bureau could not exist without a very considerable annual subsidy, since a central staff would be necessary to carry out its objects. The Delegates of the Association in the different countries have already made enquiries regarding the possibilities of subsidies from their respective Governments, and on the whole with a favourable result. Holland is ready to take the initiative, provided the other Governments shew an inclination to follow. France, Norway and Austria have already given the matter their favourable consideration. In our own country the well-known disinclination of Parliament to embark on rash adventures, such as the endowment of pure science, makes it scarcely likely that an Imperial grant will be forthcoming, but it is possible that an application to the Universities, or to the leading Scientific Societies might be successful.

It may be mentioned that Professor Went of Utrecht has already most kindly offered to establish a Bureau for Mycology (as a part of the Central-bureau of the Association) in his own Institute; from which cultures of Fungi, especially of the rare species, can be supplied.

The "Centralblatt" Lists of Current Literature.

The main topic of discussion on the morning of April 16th, was the publication of the Lists of Current Literature. It was suggested that this Department should be taken over, as from the beginning of 1904, by Dr. Field, of Zurich, who gave an interesting account of the methods adopted in the classification of new literature in the Concilium Bibliographicum at Zurich.

The members of the Association were most hospitably received in Holland; being entertained at lunch by the Dutch Botanical Society, and at dinner in the evening by some of the leading citizens of Leiden, whilst the programme of the next day included a visit to the Bacteriological Institute at Delft, where a most interesting lecture was given by Professor Beyerinck.

F. E. FRITSCH.
A. G. TANSLEY.

MACARANGA TRILOBA: A New Myrmecophilous Plant,

By Winifred Smith,

University College, London.

[With Plates V. and VI].

FROM what structural feature or combination of features are we entitled to infer that a plant is myrmecophilous, *i.e.* that it is definitely adapted to provide attractions for ants in return for protection by them? One writer considers an appropriate cavity for the ants to shelter in a sufficient sign of adaptation; another that extra-nuptial nectaries should always be present. A third thinks that the latter appeal no more to ants than to any other marauding insect with designs upon pollen, and that proteids in "food-bodies" should be offered. All look anxiously for signs of ants on the plants themselves and find these difficult to obtain in herbarium material, because the ants hurriedly leave the plants as soon as they are gathered, or desert them when they are drying. The material of *Macaranga triloba* on which the present observations were made was collected and brought home by Mr. Tansley, whose attention was drawn to the apparent myrmecophily of the plant by Mr. H. N. Ridley, the Director of the Royal Botanic Gardens, Singapore. This material consists of a few dried sprays and three seedlings (preserved in spirit), about 12 to 18 inches high, which were growing wild in the Singapore gardens. The plant seems (so far as can be gathered from the limited material at hand) to unite in itself all the essential characters of myrmecophily, *viz.* an appropriate cavity as a nesting place, a thin region which facilitates the boring of holes for ingress, and food-bodies, conceivably of a proteid nature, besides extra-nuptial nectaries—thus forming a combination only equalled by the two myrmecophilous species of Acacia (*A. cornigera* and *A. sphaerocephala*) (2) and by *Humboldtia laurifolia* (1). The tree belongs to the tropical genus *Macaranga* of the Euphorbiaceae, and is identified as *Macaranga triloba*. The seedling has hollow internodes in the woody stems (see fig. 2), one peltate leaf and a pair of stipules at each node. Of the stipules, some are caducous, some persist. When they are protecting the bud, they are erect; older ones are retroverted and become closely appressed to the stem (see fig. 1.)

The appropriate cavity is found in the hollow internodes, which are swollen in young stems. The pith seems to break down

naturally, and not to be eaten away by ants, for a transverse section shows a peripheral ring, 8 or 9 cells thick, inside the wood and bounded on the inside by continuous cell-walls. This cavity may perhaps be regarded as the result of adaptation to ant inhabitants on the part of the plant (see figures 10 and 2).

Ingress is also facilitated by the plant. Grooves run vertically up the stem from the leaf axil to the next node, and these are probably caused, as in *Cecropia* (2) by the pressure of the axillary bud on the soft young tissues and the longitudinal stretching of the stem. The grooves are somewhat wider at the upper end, but the stretching of the circumference has less effect than it has in *Cecropia*. The grooves are not present on all internodes, but in nearly all the grooves there are one, two, or three holes leading to the cavity within and placed near the end of the internode (fig 1). In some of the internodes without grooves there are holes which only penetrate a short distance and show signs of considerable cambial activity. Some of these holes are stopped by a plug of latex, possibly of caoutchouc. The latex cells, which are very prominent, have yellow, brown or red contents (see figs. 10 and 11).

In young stems there is a distinct nodal plate, but this is perforated in older material, probably by the ants, as in *Cecropia;* so that there is free communication between the internodes and a hole is unnecessary in every one.

As in *Humboldtia laurifolia* (1) and *Duroia hirsuta* (3) the food-bodies in *Macaranga triloba* are on the stipules. Here however they are found on the morphological under side, which becomes, in old retroverted stipules, the concave side where they are hidden from all but the initiated (see Figs. 1 and 3). They are of a very peculiar structure and consistency and much more work will be necessary before I can give a satisfactory account of them. They are not however unique among food-bodies eaten by ants in being abnormal, for Schimper says of the Beltian corpuscles (2): "Sie unterscheiden sich jedoch von allen bekannten Drüsen durch bestimmte Merkmale,...........nämlich durch bedeutendere Grösse, längerer Dauer, Reichthum an Eiweissstoffen, leichtes Abfallen beim Berühren." Their shape is spherical or pear-shaped, they are of a golden yellow colour, and their contents greatly obscure their structure. Absolute alcohol and clove oil cleared them somewhat and showed them to be multicellular, with external hexagonal marks, presumably cell-walls. They can be ruptured with considerable pressure under a cover-slip and then exude drops of a liquid

which does not mix with glycerine (see figs. 5, 8 and 9). It will be remembered that Francis Darwin (4) showed that the Beltian corpuscles contain oil—insoluble in glycerine but soluble in absolute alcohol. Associated with these "food-bodies" are glands resembling the Lupulin-glands of the female inflorescence of the Hop, which De Bary calls "Bladder-glands." The bladder is formed by the cuticle, which is separated from the epidermis by the secretion. In *Macaranga* there can be seen, in surface view, a plate of 8 or 9 cells, with radial and periclinal walls, below the bladder. If the multicellular food–bodies arise from these glands it must be by further division by anticlinal walls so that the circular plate of cells becomes a sphere. Satisfactory intermediate stages are wanting, but in some of the glands hexagonal markings are seen on the cuticle similar to those on the food-bodies (see figs. 4 and 6). The cuticle of the food-bodies is very tough; it resists crushing and few re-agents can penetrate it.

Nectaries are borne at the serrated tips of the leaves. They are identical with those described by Beccari in *Macaranga caladiifolia*, which species differs from the one under discussion in the shape and position of the stipules and in the absence of food-bodies in them. The nectaries in *M. caladiifolia* are cup-shaped glands found at the extremity of veins near the base of the peltate leaf (see figs. 7, 12 and 13).

Finally there were found in the internodes many ants, not only adults, but also pupae and larvae. Their presence, which is apparently an unusual feature, is probably due to the fact that the material was put into spirit within a few hours of gathering, so that the ants had no time to escape, or would not leave their pupae in the internodes and could not drag them through the holes. The ants have been identified by Colonel Bingham as belonging to an apparently undescribed species of *Cremastogaster* near *C. daisyi*, Forel.

This is the case for *Macaranga triloba* as a claimant for Myrmecophily. Of course one cannot but agree with K. Schumann when he says: "Der Beweis dass ein Gewächs als Ameisenpflanze zu betrachten ist, kann im strengsten Sinne des Wortes nur an den Localitäten geführt werden, wo dasselbe seine Heimath hat. Vor allem muss durch das Experiment gezeigt werden, dass die Entfernung der Insecten auf das Gewächs einen bemerkbar schadigenden Einfluss ausübt." Such an experiment has yet to be tried on *Macaranga triloba* in its native habitat, but the striking

combination of features found in it can only be explained as adaptive and it may therefore be regarded as fully entitled to enter the ranks of the myrmecophilous until it has been submitted to Schumann's test and has failed to justify its position.

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EXPLANATION OF FIGURES ON PLATES V. and VI. ILLUSTRATING MISS WINIFRED SMITH'S PAPER ON *MACARANGA TRILOBA.*

Plate V.

Fig. 1.—Part of stem natural size, *s*, stipules; *ap*, aperture; *gr*, groove.

Fig. 2.—Split stem to show hollow internodes. Natural size.

Fig. 3.—Concave side of stipule, *fb*, food-bodies; *c*, cavity; *a*, place of attachment to stem. (× 6).

Fig. 4.—Vertical section through bladder gland and epidermis of inside of stipule, *e*, epidermis; *pc*, plate of cells, *c*, cuticle; *bg*, bladder gland. (× 293).

Fig. 5.—Vertical section through bladder gland and food-body on inside of stipule, *fb*, food-body. (× 293).

Fig. 6.—Bladder gland, surface view. (× 355).

Fig. 7.—Vertical section through nectary. (× 80).

Fig. 8.—Food-body, surface view, cleared in absolute alcohol and clove oil. (× 134).

Fig, 9.—Large food-body, crushed, exuding oil drops in glycerine. (× 60),

Plate VI.

Fig. 10.—Transverse section through part of hollow stem with partial perforation repaired by latex plug (*l.p.*) and cambium; *m*, Pith; x^2 secondary Xylem; *c*, cork (Diagrammatic). (× 60).

Fig. 11.—Transverse section through part of hollow stem to show complete perforation; lettering as in Fig. 10. (Diagrammatic.) (× 33).

Fig. 12.—Surface view of nectary showing its relation to vascular bundles of leaf. (× 46),

Fig. 13.—Under side of leaf showing system of veining and position of nectaries, *n*. Natural size.

THE SEEDLING OF *TORREYA MYRISTICA*,

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[WITH PLATES VII. AND VIII.]

TORREYA is a small and little known genus, which in conjunction with *Taxus*, *Cephalotaxus* and *Podocarpus* forms the group of the Taxineae.

Torreya myristica, syn. *californica*, locally known as the Californian nutmeg, is found in the ravines of the Sierra Nevada in California, where it grows to a height of 40 to 50 feet.[1] Other species are found in Japan and the Himalayas. The tree is an evergreen and its foliage recalls that of the common yew, but the leaves are larger and longer. The plum-shaped drupe-like fruit, about one and a half inches long, consists of a single seed enclosed in a fibrous fleshy envelope, which, when ripe, is of a green-brown colour. The tree does not usually thrive in Great Britain, and the production of fertile seed is rare, but an exception is found in the gardens at Orton Longueville, near Peterborough, where a large tree exists in a flourishing condition and produces fertile seeds. Two of the three seedlings described in this paper were germinated there, and an opportunity of examining them was afforded by the kindness of Mr. A. Harding, the head gardener, who sent them to Professor Oliver.

These two seedlings, represented in Pl. vii, Figs. 2 and 3, were sown, with the fleshy covering still on, at the time when the seeds were ripe, in November, 1900, and were gathered on May 31st, 1902, and June 15th, 1902, so that they were respectively eighteen and nineteen months old. The third seedling (Pl. vii., Fig. 1) came from Kew, and was sown in January, 1895, and gathered in May of the following year, being thus sixteen months old. The Orton seedlings were much more advanced than this; their epicotyls had reached heights of five and eight inches respectively, and there was a great development of secondary thickening both in root and stem. The one from Kew had an epicotyl only two inches high, and the smaller amount of thickening present made the specimen far more useful for anatomical purposes. In all three cases all trace of the fleshy covering was gone.

[1] Veitch, Manual of Coniferae, p. 309.

Torreya seedling recalls vividly that of *Gingko* in appearance. In each the cotyledons are hypogeal structures, thick and fleshy, and bearing very little resemblance to leaves. (Pl. viii., Figs. 2, 3 and 4). The petioles, starting from either side of the hypocotyl, bend round, each through 90°, to meet in a position half-way between, and become closely adpressed even outside the seed. (Pl. vii., Figs. 1, 2 and 3, Pl. viii., Fig.4). There is a considerable variation in the length of petiole outside the seed. In the two Orton specimens (Pl. vii., Figs. 2 and 3) this was only a few millimeters, while in the one from Kew there was a length of nearly 4 cm.

Within the seed it is difficult to say where the petiole ends and the lamina begins and there is also a great variation in the form of the adpressed cotyledons (Pl. vii., Fig. 2, and Pl. viii., Figs. 3 and 4), those of one seedling being sickle-shaped, of another broadening to a spathulate apex and of the third being almost tubular.

The appearance obtained on breaking open the seed and dissecting out the cotyledons, leaving them lying in position, is most striking: The cotyledons, which are of a vivid green colour, lie in the white endosperm, into which penetrates in all directions the hard black nucellus. The endosperm is cut up into a body of very irregular shape owing to this rumination of the intrusive nucellus, which, brown at first, has become black at this stage. It is possible that the rumination of the endosperm may account for the variations in shape of the cotyledons and for other points about them which will be dealt with later.

Form of the Cotyledons.

The cotyledons having the simplest form were those from the seedling shewn in Pl. vii., Fig. 2. The portion within the seed was 35 mm. long and each cotyledon possessed a petiole-like region and a spathulate expanded apex, which may be called for convenience the lamina. The two cotyledons were similar in all respects and were free from each other throughout. The epidermis, however, of each, on the side directed towards the other, was in close contact with the endosperm, and probably was performing an absorptive function.

Each cotyledon had a single vascular bundle which ran the whole length of the cotyledon without dividing, merely broadening in the laminar region. The anatomical details will be considered later.

In the seedling from Kew, (Pl. vii., Fig, 1 and Pl. viii. Figs. 1, 2 and 3), the cotyledons were tubular and fused together by their

morphological upper surfaces throughout the greater part of the region within the seed.

In Pl. viii. fig.. 1, A represents one cotyledon, which is about half the length of the other. The tip of A is only free from the other cotyledon during the last ½ mm. of its length ; it also shows a tendency to lobe in its free region and the vascular bundle divides. The other cotyledon B begins to form a lobe C, 6 mm. behind its apex; the lobing in this case is complete, one branch of the the bundle passing to C.

In the third seedling, (Pl. vii., Fig. 3 and Pl. viii., fig. 4), the apices of the cotyledons were bent into a sickle shape and the petioles, free for about half their length, became fused before this region was reached. Here again one cotyledon was much shorter than the other, and both showed a tendency to lobing in the behaviour of the vascular bundle, which widened and seemed about to separate into two portions in each.

Strasburger[1], in his work on the Coniferae and Gnetaceae, mentions this tendency for the cotyledons to be fused and lobed in Cycads and in *Ginkgo*, and it is especially interesting to find the same characters in two out of three specimens of *Torreya*, another primitive genus.

In *Ginkgo biloba* the cotyledons remain underground in the endosperm and only the basal parts project from the seed-shell. They are not fully fused at their apex, but they adhere so closely together that they cannot be separated without tearing the tissue ; and what especially recalls the Cycads is the fact that the extreme tips of the cotyledons are swollen and show a feeble indentation, just as Schacht[2] figured for *Zamia spiralis*. In *Torreya Myristica* the lobing in one instance is much more marked than in *Ginkgo*, and fusion of the cotyledons was found in all three seedlings.

It is hardly possible to say what may be the importance of this tendency to lobe. The cotyledons are no doubt influenced by space relations within the seed, and the irregular form of the endosperm may cause the variation in shape and lobing of the cotyledons in this case ; for in other cases of ruminated endosperm, as among the Palms and in the nutmeg, the lobing of cotyledons is frequent.[3] On the other hand in the case of *Anona*, where there is a ruminated endosperm, there is no trace of lobing in the cotyledons.

[1] Die Coniferen und die Gnetaceen, p. 320.
[2] Schacht, Der Baum, p. 53.
[3] Tschirch, Ann. du Jard. Bot. de Buitenzorg, Vol. IX., p. 165, 1890.

The *Epicotyl* is clothed at first with scales having a $\frac{2}{5}$ phyllotaxy, and these, as one ascends, pass over into foliage leaves having the same arrangement.

There is a strong primary tap root which bears many laterals.

Anatomy of the Root.

The main root and laterals are alike diarch.

The protoxylem elements are separated from the metaxylem plate of primary xylem, and from each other, by large parenchyma cells with contents (Pl. viii., fig. 5). In each seedling there was a good deal of secondary wood formed.

The secondary phloem is remarkable only for its very large fibres, in the walls of which crystals of calcium oxalate are imbedded. The number of these fibres become fewer as the transition region is approached.

The pericycle is many-layered, and the outermost layer divides tangentially to form a periderm. There is in the cortex the same layer of cells with huge lenticular thickenings which is found in a similar position in *Taxus*. These are seen in longitudinal section to be due to a continuous strap of thickening running round the radial and horizontal walls of the cells of this layer, and with a lenticular transverse section. Within this is the true endodermis with typical dots on the radial walls in transverse section; a much less striking feature than the "false endodermis."

Transition Region.

The whole passage from typical root-structure to the cotyledon-node occupies 3 mm. in one, and 5 mm. in the other of the two cases in which the passage was followed. At the base of this region we have typical root structure and no secondary xylem in the positions outside the protoxylems. These consist at this level of about a dozen elements each, much smaller than those of the metaxylem; outside these are a few parenchyma cells, and outside these again a cambium is beginning (Pl. viii., figs. 5 and 6.). The protoxylem elements, which below were attached to the metaxylem plate, move outwards one by one, and are obliterated among the parenchyma cells within the cambium (Fig. 5.).

The first sign of approaching stem structure is found in the appearance of a central pith and the breaking up of the root plate, and portions of this primary root xylem are close up against the ring of secondary (Fig. 7.). The two largest of these patches

are in the positions of the late protoxylem groups, *i.e.* in the positions from which the cotyledon traces will go out. Secondary xylem is now formed in these two places by the cambium, and the metaxylem patch is in contact with secondary xylem here, as elsewhere at the periphery of the pith (Fig. 8). The phloem is continuous across the former gap, while the true endodermis and the "false endodermis" with globular thickenings alike disappear. (The outermost layer of the pericyclic periderm has here elongated radially, and has also become suberized, so that at first sight it might be taken for an endodermis.)

Character of the Cotyledon-Trace on its passage out.

The cotyledon trace in the hypocotyl corresponds in position with that of the root protoxylem. The trace consists of some secondary xylem formed from the trace-cambium, some primary, and some protoxylem elements which stretch inwards in bands and come in contact at certain places with the continuations of the root plate; these I propose to call for purposes of convenience and description, metaxylem strands (*mx*). In the transition region they have the position already described, and consist of scalariform tracheides, but when the cotyledonary bundles are formed those opposite to it, *i.e.*, in the two root-protoxylem regions, soon shew a change, so that among them, and at first between them and the secondary xylem of the ring, later between them and the true protoxylem of the cotyledon trace, smaller elements appear, which are seen in longitudinal section to be spiral and annular. This stage is shewn diagrammatically in Pl. viii., figs. 8 and 9. The appearance of the strand as shewn in fig. 8, reminds one of an exarch bundle, and the presence, as will be described later, of a large quantity of centripetal xylem in the lamina and petiole of the cotyledon, would seem at first to lend a good deal of significance to this state of affairs, and in consequence the strand was followed carefully into the cotyledon petiole, by means both of transverse and longitudinal sections. In longitudinal section these strands are seen to consist more and more of spiral and annular elements; till, as the cotyledonary node is approached, and they finally pass out into the petiole, still in contact with the trace-protoxylem, they are entirely formed of typical protoxylem elements.

Summary of Transition.

The root-protoxylem dies out below the cotyledonary node; and the protoxylem which accompanies the cotyledon trace out-

wards would seem to have a double origin, one portion corresponding to the strand (*mx.*) which is directly inserted upon the root metaxylem, and the other seeming to belong more intimately to the cotyledon trace (*px.* in Figs. 10 and 11.).

Thus *Torreya* does not fall into any of the cases of typical diagrammatic passage from root to stem. A possible explanation of the "dying out" of the root protoxylem is that the xylem connection between the root and the cotyledons was made at a time when, and in a region where, elongation had ceased and possibly growth in thickness was taking place. This would account for a region devoid of spiral and annular elements.

The two seedlings examined for this transition gave practically identical results. Of the two it was easier to follow in the younger seedling (that from Kew), but in each there was a great quantity of secondary xylem present which increased the difficulty.

Anatomical Structure of the Cotyledon.

At the base of the petiole the protoxylem is central (fig. 11.). The more internal of its elements are much crushed and these can be traced down to the "metaxylem" strand *mx*, while other elements not crushed are in contact with the primary and secondary xylem of the bundle. At this level there is only a very occasional centripetal xylem element, while similarly very rare transfusion-tissue elements are found on the flanks of the bundle. The amount of both increases very greatly as the bundle is traced upwards, until half way up we have a state of affairs which recalls that in the cotyledon of *Ginkgo* or *Cephalotaxus*.

Before, however, this level is reached, the bundle changes in appearance somewhat, having in transverse section an approach to a kidney-shape (fig. 12), with crushed protoxylem in the concavity, and a certain amount both of centripetal xylem and transfusion-tissue present.

The centripetal xylem attains its maximum development half way up the cotyledon, while the amount of transfusion-tissue goes on increasing, until finally, at the apex, it is the only vascular tissue left.

Pl. vii., figs. 4 and 5, shew respectively a transverse and a longitudinal section about the middle of the cotyledon. By combining the two, it will be seen that the xylem of the bundle is composed of the following:—Starting from the dorsal side, we have secondary tracheides which show the typical Taxinean

type of thickening (a combination of scalariform thickening and bordered pits), then scalariform metaxylem elements and next protoxylem elements which are loosely spiral and annular. To the inside of these again we get long narrow tracheides, of greater diameter than the protoxylem. Some of these have loose thickenings almost of the character of protoxylem thickenings, but the majority are scalariform, or sometimes pitted. In many places there can be seen a complete transition from these, through tracheides which are shorter but of greater diameter, to the scalariform and pitted elements of greater diameter and almost cubical form which make up the transfusion-tissue here. These transfusion-elements are found ventrally, and in longitudinal section are seen to occur for the most part in vertical rows, the row being interrupted occasionally by a parenchyma cell exactly similar in form, but with no thickenings. It certainly looks here as if the transfusion tissue in this position were being formed from the parenchyma outside the bundle.

According to Mr. Worsdell, however, the presence of complete transition in size and other characters which is found between the elements of the centripetal xylem and the transfusion-tissue is an argument against this, and supports the origin of the transfusion-tissue as a direct extension of the centripetal xylem.[1]

In one pair of cotyledons (Pl. vii., fig. 2) there was an expanded region near the tip of each which might fairly be described as a lamina. In this region the bundle was very greatly elongated and there was a great development of transfusion-tissue on it's flanks, shewing a tendency to extend on either side in a dorsal direction. It was almost absent in the central ventral position. There were also a good many centripetal xylem elements present. At the tip the transfusion-tissue had increased enormously in amount, and was now found completely enclosing the flanks of the bundle and extending to take up a central dorsal position. In two of the seedlings there was a lobing (in one case incomplete) at the tip of the cotyledon; in these the bundles divided just before the lobing took place, and the transfusion-tissue of each branch behaved exactly as above. In one case one of the lobes showed a cambium present on the dorsal side of the bundle, and a few secondary elements were formed from it, so that finally one had a concentric bundle with the original protophloem in a central position.

[1] W. C. Worsdell on Transfusion-Tissue. Trans. Linn. Soc., Dec., 1897.

Epicotyl. I was unable to find any trace of centripetal xylem in the Epicotyl. The stem is clothed with leaf bases, and the stele is composed of leaf-trace bundles which keep their identity and are to be seen in connection with their own particular leaf bases. This is particularly well seen as the apex is approached.

Immediately above the cotyledonary node the stem bears scales; these give place above to foliage leaves and the transition between the two is gradual and complete. I examined the scales to see if centripetal xylem were to be found there, but neither here nor in the foliage leaves, either of the seedling or of the adult, was any trace to be seen. In the scales an occasional transfusion-element was present in a ventral position, in the leaves there was a considerable development on the flanks of the bundle, but none in a central position.

To summarise: the important points in the seedling of *Torreya myristica* would seem to be the retention of certain primitive characters. In the anatomy of the cotyledons we have such a primitive character as the presence of centripetal wood, while the lobing and adhesion of the cotyledons is a feature which *Torreya* has in common with other primitive genera, such as *Zamia* and *Ginkgo*.

The somewhat exceptional method of transition from root-structure to that of the hypocotyl and cotyledon-petioles, is also of interest.

In conclusion I should like to take this opportunity of thanking Professor Oliver for his help and the interest he has taken in the work.

DESCRIPTION OF FIGURES ON PLATES VII. AND VIII. ILLUSTRATING MISS CHICK'S PAPER ON THE SEEDLING OF *TORREYA MYRISTICA*.

PLATE VII.

Fig. 1.—Seedling from Kew, 16 months old ($\times \frac{1}{2}$).
Fig. 2.—Seedling from Orton, 18 months old ($\times \frac{2}{3}$).
Fig. 3.—Seedling from Orton, 19 months old ($\times \frac{3}{10}$).
Fig. 4.—Transverse section of the cotyledon-bundle about half way up from seedling in fig. 2 ($\times$ 142).

Trf. transfusion tissue.
Cp.x. centripetal xylem.
Px. protoxylem.
X^1. centrifugal primary xylem.
x^2. secondary xylem.

Fig. 5.—Longitudinal section of cotyledon-bundle in same region as fig. 4 ($\times$ 125). Same lettering.

PLATE VIII.

Fig. 1.—Diagram of cotyledons of seedling in Pl. vii., Fig. 1.
A. the shorter cotyledon.
B. the longer cotyledon with its lobe C.

The small diagrams show the appearance of the cotyledons in transverse section at their respective levels.

Fig. 2.—Cotyledons of the same seedling seen from both sides. (Region within the seed.)

Fig. 3.—Cotyledons of same seedling with petioles attached.

Fig. 4.—Cotyledons of seedling shewn in Pl. vii., Fig. 3, dissected from the seed.
a[1]. *b*[1]. the two cotyledons.
w.x.y.z. transverse sections taken along the lines similarly lettered.

Fig. 5.—Transverse section at the base of the transition region (×280) The protoxylem is shewn as a group of scattered elements. These become obliterated above.

The same stage is shewn diagrammatically in fig. 6.

Figs. 6-12.—Series of diagrams from the base of the transition regions tracing the cotyledonary vascular bundle into the petiole. In figs. 6-10 the diagrams are bounded by the outer limit of the pericycle.
ph. phloem.
x^2. secondary xylem.
cb. cambium.
rt. px. root protoxylem.
rt. mx. root metaxylem plate.
mx. metaxylem strand (continuous with *rt. mx.* of Fig. 6), which becomes attached to the cotyledon-bundle and of which the elements in Fig. 8 are partly spiral and partly scalariform, and in Figs. 10, 11, and 12. are entirely spiral and annular.

Fig. 12.—Cotyledon-bundle in the petiole. Protoxylem and traces of metaxylem shewn in the concavity of the kidney-shaped bundle.
cp. x. centripetal xylem.

ON THE LEAF-STRUCTURE OF *CORDAITES*.

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(With Plate IX.)

The specimens upon which this note is based were derived from the well-known Grand 'Croix nodules of the French Stephanian. They include one short series of transverse, and a few detached transverse and longitudinal sections of several Cordaitean leaves, probably identical with the form which M. Renault has correlated with *C. principalis* of Saint-Etienne[1].

Though no striking point of novelty arises from their exami-

[1] B. Renault. Structure comparée de quelques tiges de la Flore Carbonifère, pl. 16, fig. 6., p. 301. Cours de Bot. foss. I., pl. 12, fig. 6.

nation, they present some features of interest; whilst the state of preservation is unusually good, especially in those tissues which generally leave much to be desired in this respect.

The general type of the leaf, which is that figured by M. Renault under the name *C. principalis*, is shewn in phot. 2, plate IX. It is dorsiventral in structure, having the vascular bundles arranged in one plane, at an average distance apart of ·45 mm. Each bundle is enclosed in a double sheath and accompanied by strands of sclerenchyma above and below. Large strands of the same sclerenchyma alternate with the vascular bundles on the lower face, whilst above there are three or four small and irregular groups just below the epidermis.

The majority of the bundles are parallel and equidistant, and the branching, which appears to occur but seldom, is dichotomous[1], the two strands moving very slowly apart. When commencing to divide, the phloem is separated into two groups by an intrusion of the inner sheath, the protoxylem remaining as one (see phot. 4.); the protoxylems then split and move slowly apart, the inner sheath attaching itself to the centripetal xylem before either the outer sheath or sclerenchyma above shew signs of division. This behaviour is more striking than in the case of the recent Cycads, *e.g.*, *Zamia* or *Ceratozamia*, where the veins are similarly arranged, and in which the phloem also divides first into two free groups, but the above-described behaviour of the inner sheath is less pronounced. In *Myeloxylon radiatum*, the petiole of a *Medullosa*, where the individual bundle is of similar organization, the division appears to originate sometimes in the phloem and sometimes in the xylem.

The parenchyma of the leaf is differentiated into palisade above and spongy parenchyma below. In sections in which the bundle is cut transversely this distinction does not appear very striking, the palisade cells are almost hexagonal and closely packed, while the spongy parenchyma appears similar but rather more irregular or lacunar. Between the two on each side of the bundle are a few clear cells with thin walls, elongated transversely, and although hardly specialised enough to be called accessory transfusion-tissue, they appear in some cases to merge into the cells with pitted walls at the sides of the bundles.

[1] Cf. Lignier, "La Nervation des Cycadées est dichotomique," Assoc. Française pour l'avancement des Sci., Congrès de Caen, 1894, where he demonstrates the fact that the branching of all the nerves in Cycads is truly dichotomous.

In a section at right angles to the above, and nearly parallel to the bundles (fig. 7), the differentiation of the leaf comes out more clearly; the palisade cells are broad but regularly arranged in rows, the number of which differs according to the angle of the section, but averages roughly at four; the cells of the bottom row of palisade, separated from one another by slit-like lacunae (Fig. 7), abut, often in pairs, on the large cells of a row which in its turn rests on the elongated cells appearing between the palisade and the spongy parenchyma; this last is composed of irregular cells chaining together and forming a highly lacunar tissue. The stomates were not sufficiently well preserved for description, but there are indications that they were frequent on the lower surface.

In sections parallel to the leaf surface, which cut the bundles in median longitudinal section, the parenchyma runs in bands from bundle to bundle, separated by lacunae; these cells are the elongated ones described above, and are figured by Renault[1], while tangential sections of the bundle cut the palisade or spongy parenchyma as the case may be.

It is, however, in the bundles themselves that the chief interest lies. They are of the type usual in *Cordaites*, with well marked protoxylems and a wedge of centripetal xylem above (phot. 3 and 4, fig. 5, pl. IX.), the average diameter of the protoxylem being 10μ. and of the large centripetal xylem about $50\ \mu$. In longitudinal sections (see fig. 6) the protoxylem was seen to consist of well marked spiral elements, next to them are variously banded scalariform tracheides, and the largest one or two elements are closely pitted with five or six rows of bordered pits exactly similar to the elements of the secondary wood of the stem. The centrifugal xylem usually described is entirely absent from all bundles in these leaves. The deceptive cells in phot. 3 are clearly seen in the original section to be crushed and contents-bearing phloem-elements lying next the xylem-parenchyma somewhat obliquely, so that when the rest of the tissue is in focus they appear dark and thick-walled; but when they are separately focussed they are seen to be small thin-walled elements, quite similar to the rest of the phloem, next to which they are lying.

That the absence of centrifugal xylem is a general character of this leaf is probable, as there seems no reason to suppose that these sections are specially near the tip or margin, in which case we might expect such a reduction in the bundle as occurs in recent

[1] Renault, "Sur quelques Tiges," pl. 16, fig. 9.

Cycads. All the bundles in these sections, however, are essentially similar, and, with one exception, are running practically parallel, as is shewn by the distances between each pair of bundles in the different sections of the series.

The cells of the xylem-parenchyma are large, thin-walled, and somewhat oblong in shape; sometimes, as in phot. 3, a single layer of large size fills the space between the protoxylems and the inner sheath, or as in figure 5, there may be two or even three layers of smaller cells between the two sets of hard tissue. The protoxylem is separated from the phloem by two or three large and irregular parenchyma cells. In longitudinal section the xylem-parenchyma is elongated and thin-walled, the transverse walls being slightly thicker than the others.

The phloem consists of small square elements, a few of which have structures suggestive of protoplasmic contents and nuclei; in longitudinal section the phloem shews delicate oblique walls on which we have not been able to detect sieve-plates.

The bundle sheath is well developed and is composed of two types of tissue, forming an inner and outer sheath. The outer sheath consists of two or three layers of large cells which touch the sclerenchyma above and below the bundle (phot. 3 and 4, fig. 5). They are more largely developed on the upper side and sometimes the cells between the xylem and upper sclerenchyma are of considerable size. At the sides the large cells of the outer sheath are adjacent to the palisade and spongy parenchyma, from which they are quite distinct, but in the middle, *i.e.*, on the flanks of the bundle, the outer sheath-tissue sometimes shews a tendency to become merged with the adjacent elongated middle tissue of the leaf. The inner sheath lies within the outer, closely fitted to it, the cells of the inner sheath form an arc round the phloem and attach themselves to the flanks of the most centripetal xylem-elements, where five or six of them frequently form a group on either side. The cells of the inner sheath are small and exceedingly thick-walled, recalling sclerenchyma in transverse section (phot. 3 and 4., fig. 5, *ss*). In longitudinal section (fig. 6) they are seen to be long and straight, their thick walls pitted with a single row of very well-marked bordered pits; they appear much more like true xylem than the transfusion-tissue of recent Cycads, to which we will compare them later. The outer sheath, on the other hand, consists of larger cells with thinner walls, also pitted with bordered pits, although in a more irregular fashion (fig. 6, *s.*); those which abut

directly on the upper side of the centripetal xylem sometimes have quite thin radial walls as seen in transverse section, but as the nature of their markings is uncertain the outlines of these cells alone are given in the longitudinal section (fig. 6, *si*).

In seeking to explain the sheath it is natural to turn to the recent Cycads for help, and we find in Worsdell's[1] paper on transfusion-tissue that in support of his view of its origin from centripetal xylem he mentions the cotyledons of *Cycas* as having more or less scattered transfusion-tracheides with bordered pits, which he considers are derived from the centripetal xylem. He follows Lignier[2] in tracing transitions between the normal transfusion-cells near the bundle and the xylem, and in considering the first to be derived from the xylem, but differs from him in considering the "accessory transfusion-tissue" of the leaf blade as a distinct and separate development on the part of the mesophyll of the leaf.

It is possible that in *Cycas* (and very likely the same may hold good of other Gymnosperms), in addition to the transfusion-tissue which Worsdell has derived from centripetal xylem, and wbich, since it was presumably the first to appear in evolution, may be called "primitive transfusion-tissue," on the one hand, and to the accessory transfusion-tissue of the lamina, which may be called "mesophyll-transfusion-tissue," on the other, there is a third category of transfusion elements, developed from the parenchyma of the mid-rib in connexion with the primitive, which may be called "peridesmic transfusion-tissue," on account of its origin from the parenchyma surrounding the bundle. For instance, in *C. Seemanni* transverse sections of the mid-rib shew a large development of transfusion-elements scattered widely in the ground-tissue and passing almost insensibly into it; first there are the true transfusion-tracheids with bordered pits flanking the centripetal xylem and even circling round the bundle and appearing outside the phloem; secondly, mixed with these are other elements which resemble the first, except that their pits are faintly bordered; and thirdly others again with simple pits shewing transitions into those with loose reticulations far from the bundle. The third of these categories distinctly suggests a phylogenetic origin from the parenchyma of the mid-rib, but the presence of the transitional elements

[1] W. C. Worsdell, on "Transfusion-tissue." Trans. Linn. Soc. 1897, p. 307.

[2] Lignier, "La Nervation téniopteridée des folioles de Cycas et la Tissu de transfusion." Bulletin de la Soc. Linn. de Normandie, sér. IV., tome VI., fasc. 1, 1892.

makes it clear that no sharp histological line can at present be drawn between it and the first or "primitive" type.

In the fossil *Cordaites* the transfusion-tissue is more compact and forms two definitely organised sheaths. It is possible that the inner sheath abutting so intimately upon the centripetal xylem, may represent but little modified elements of it, and thus be primitive transfusion-tissue, while the outer cells may be really phylogenetically a parenchyma sheath which has acquired bordered pits and is thus peridesmic in origin.

The completeness of the sheath, its direct attachment to the centripetal xylem, and the tracheal nature of its walls and pittings, it may be conjectured, present a primitive stage in the development of transfusion-tissue from centripetal xylem, and is an interesting example of the way in which this wood seems to have more than "held its own,"[1] in the leaf when ousted from the stem by the centrifugal development.

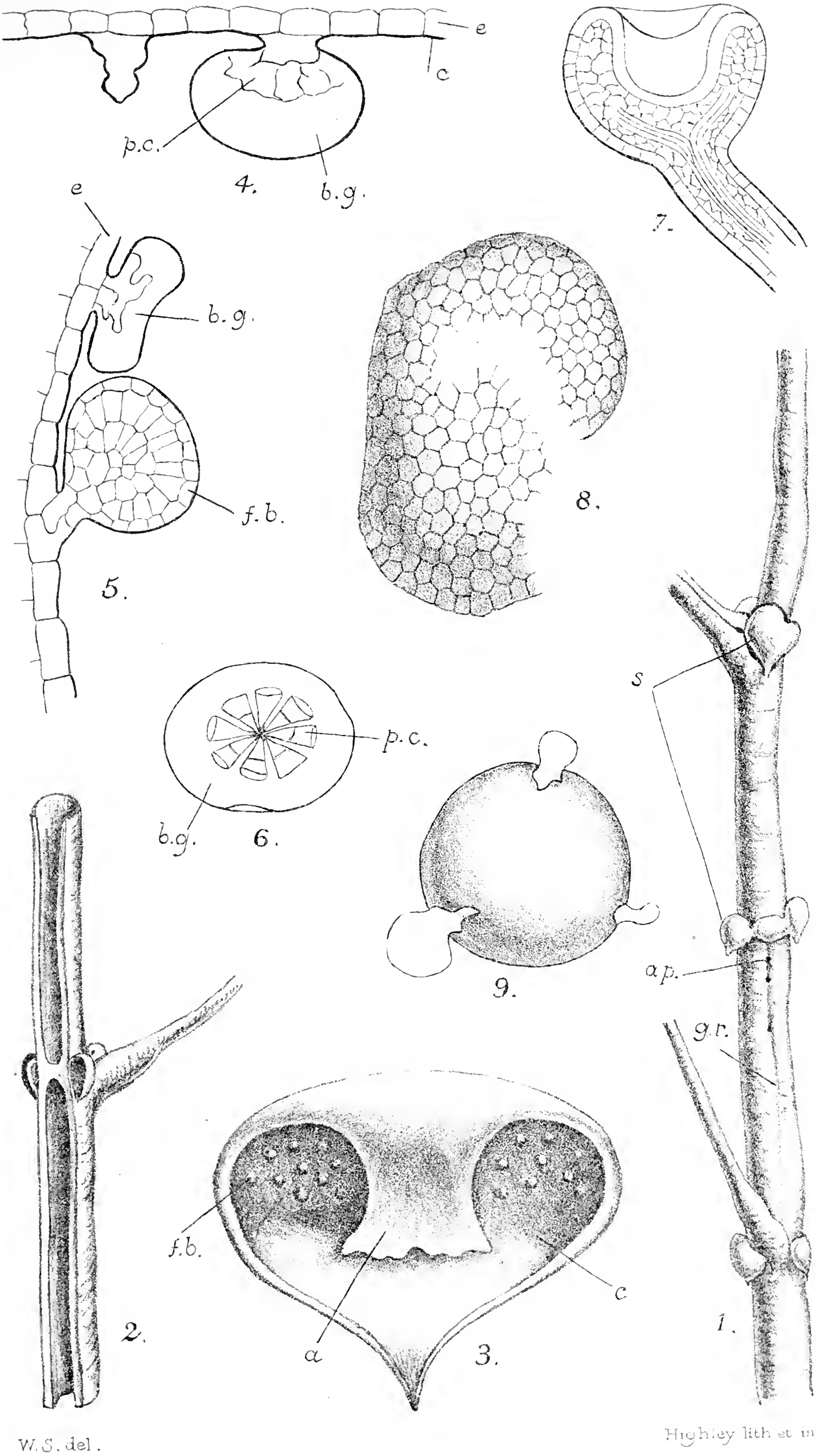
A careful comparison of our preparations with Renault's figures[2] of *C. principalis* leads to the conclusion that the "partie centrifuge du faisceau" there figured may perhaps be identical with the sheath here described. Renault's sections correspond perhaps to a somewhat different type of preservation in which the softer elements of the bundle were lost; he does not shew any phloem or xylem-parenchyma, and it is more than likely that in his slides the inner sheath was separated from the outer, and, the phloem being absent, was interpreted as centrifugal xylem such as occurs in other species of *Cordaites*, *e.g.* *C. lingulatus* (phot. 1). It appears then, as M. Renault has stated, that these sheath-cells are elements of the wood, though it seems probable that they are to be considered as derived from the flanks of the *centripetal* xylem rather than constituting the centrifugal wood in this particular case.

That the two leaves are identical and ours therefore *C. principalis* is, as we have said, strongly suggested by the comparison of the figures (phot. 2, with Renault's fig. 6, pl. xvi.), when it will be seen that our leaf resembles *C. principalis* entirely in its arrangement of vascular and sclerotic tissues, upon which Renault[3]

[1] D. H. Scott, "The Old Wood and the New." NEW PHYTOLOGIST, February, 1902, p. 29.

[2] Renault, Sur quelques tiges, pl. xvi., fig.. 6

[3] "Sur quelques tiges," p. 301. "La feuille se distingue par trois ou quatre petites bandes de tissu hypodermique placées entre les bandes principales qui accompagnent les faisceaux vasculaires à la face inférieure il n'y a qu'une seule bande d'hypoderme entre deux nervures, mais elle est plus considérable."



W. S. del.

Highley lith et imp

Smith—Macaranga Triloba.

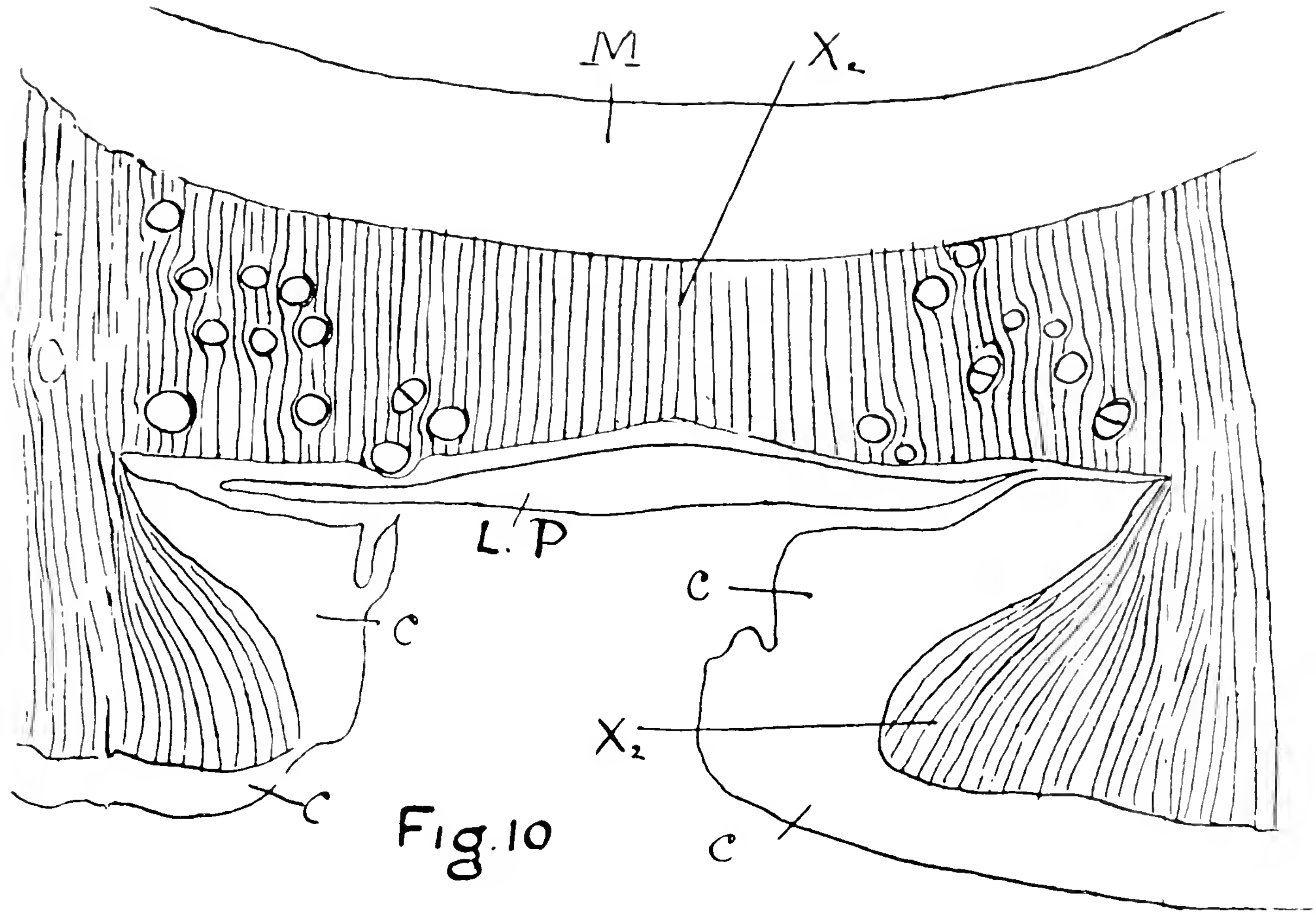


Fig.10

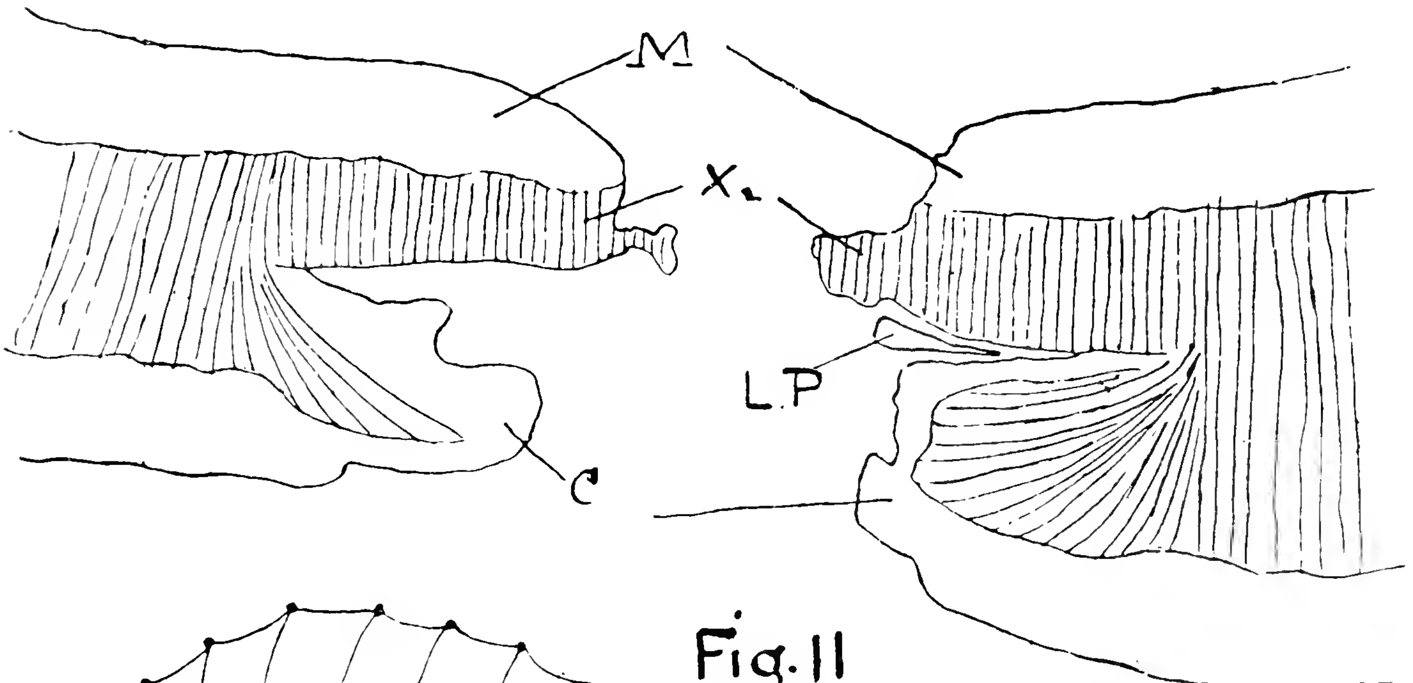


Fig.11

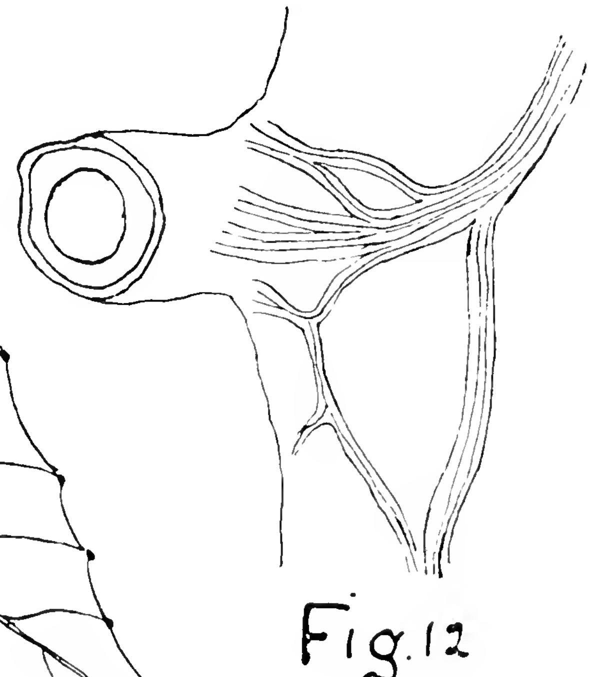


Fig.12

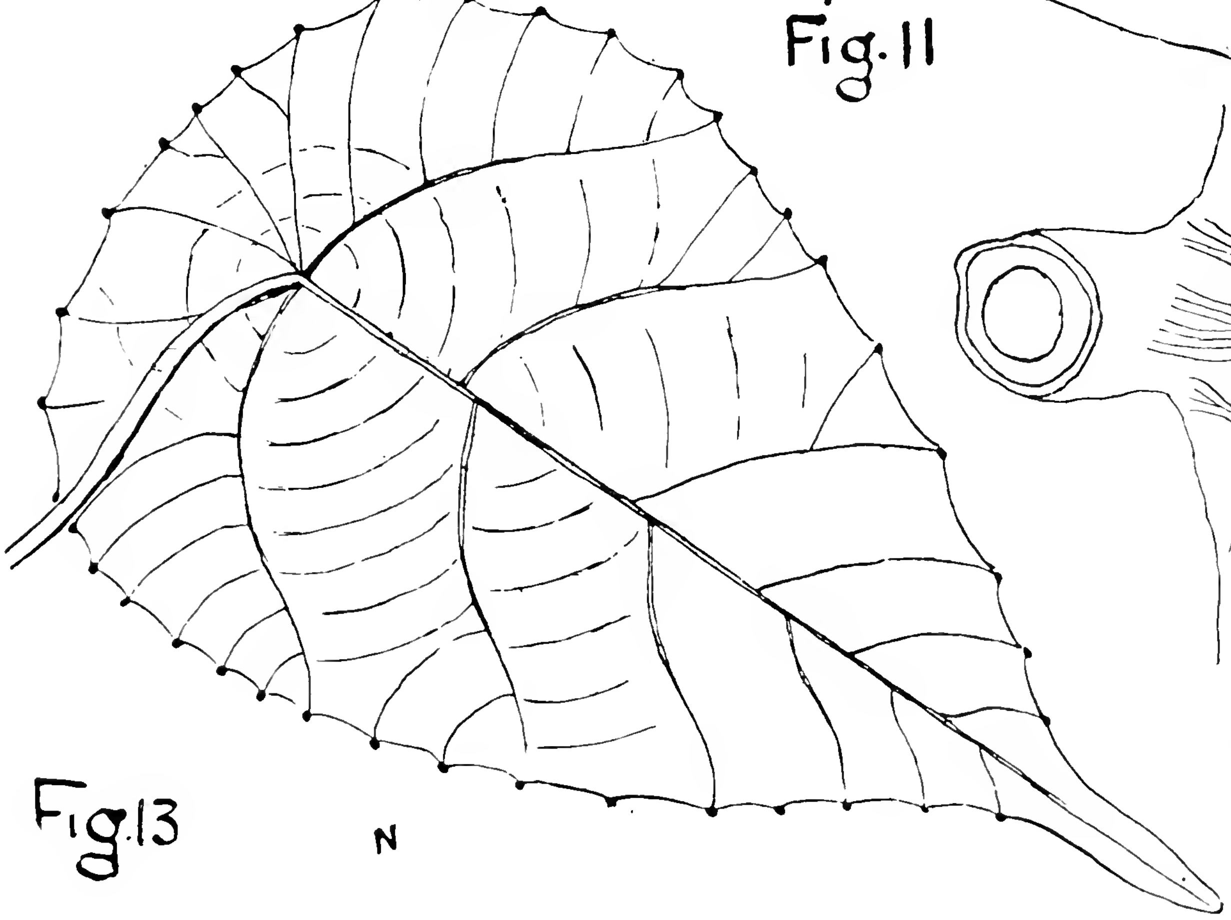
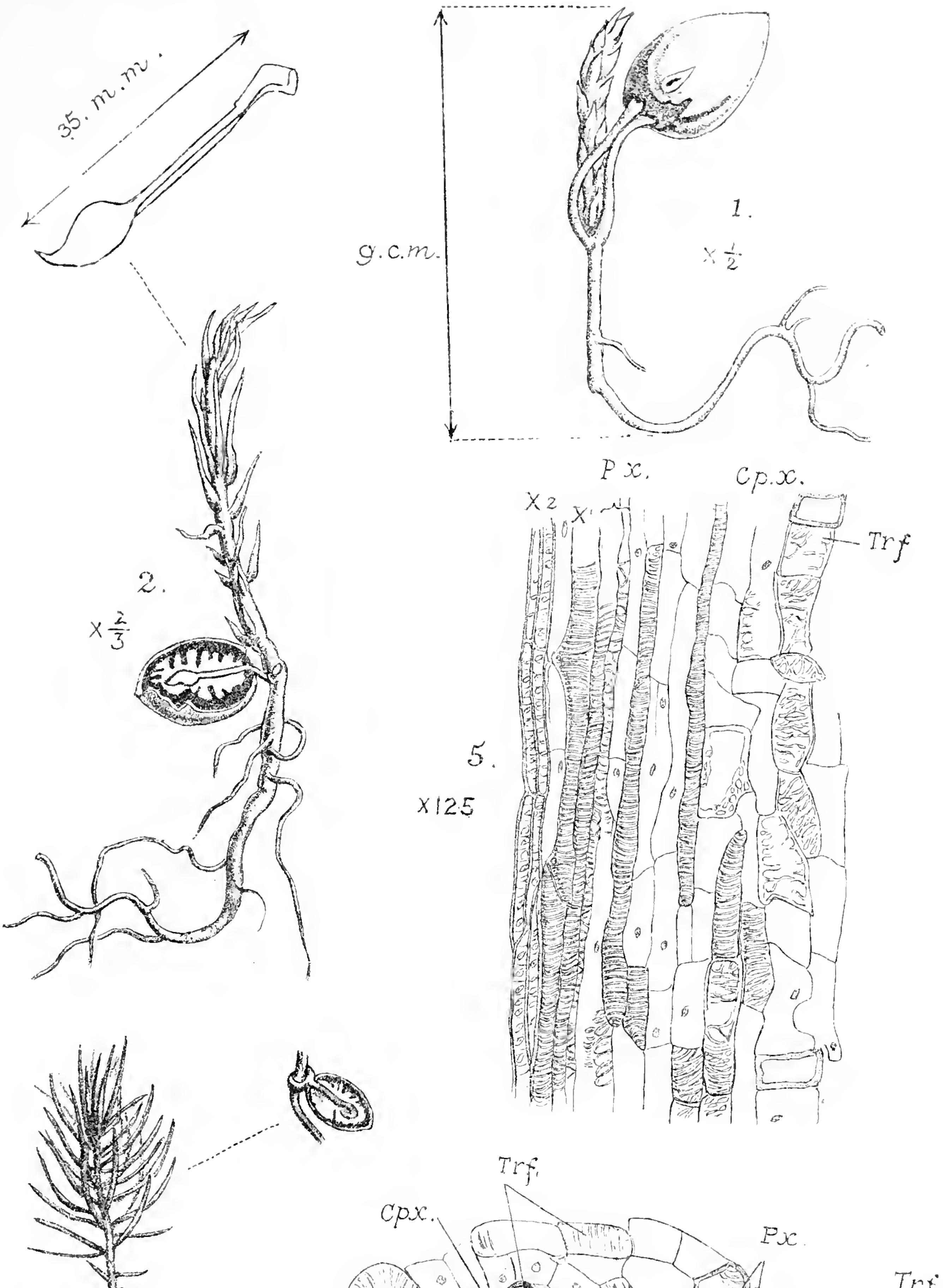


Fig.13

W.S. *del.*

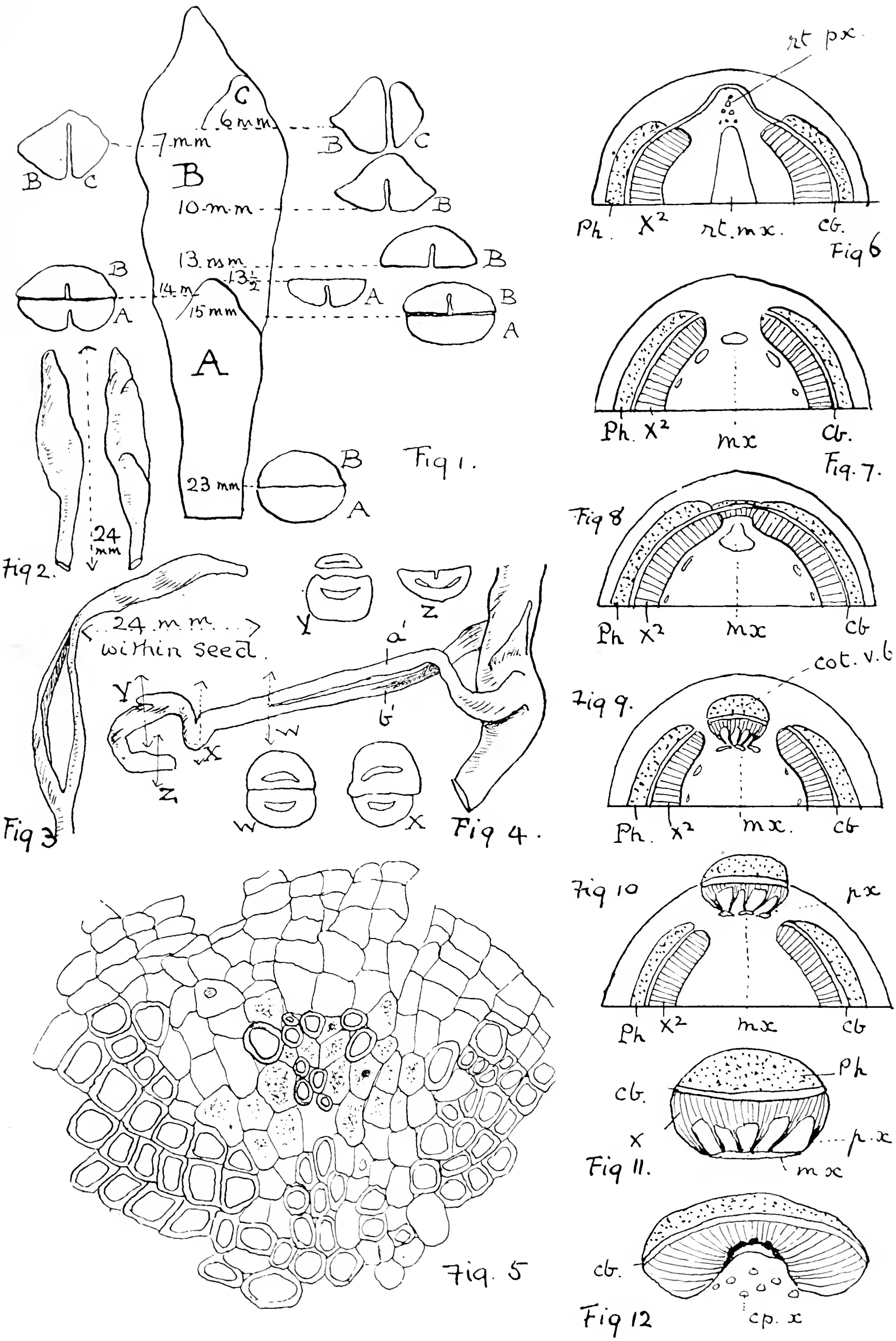
SMITH—*MACARANGA TRILOBA.*



E.C. et M.C. del.

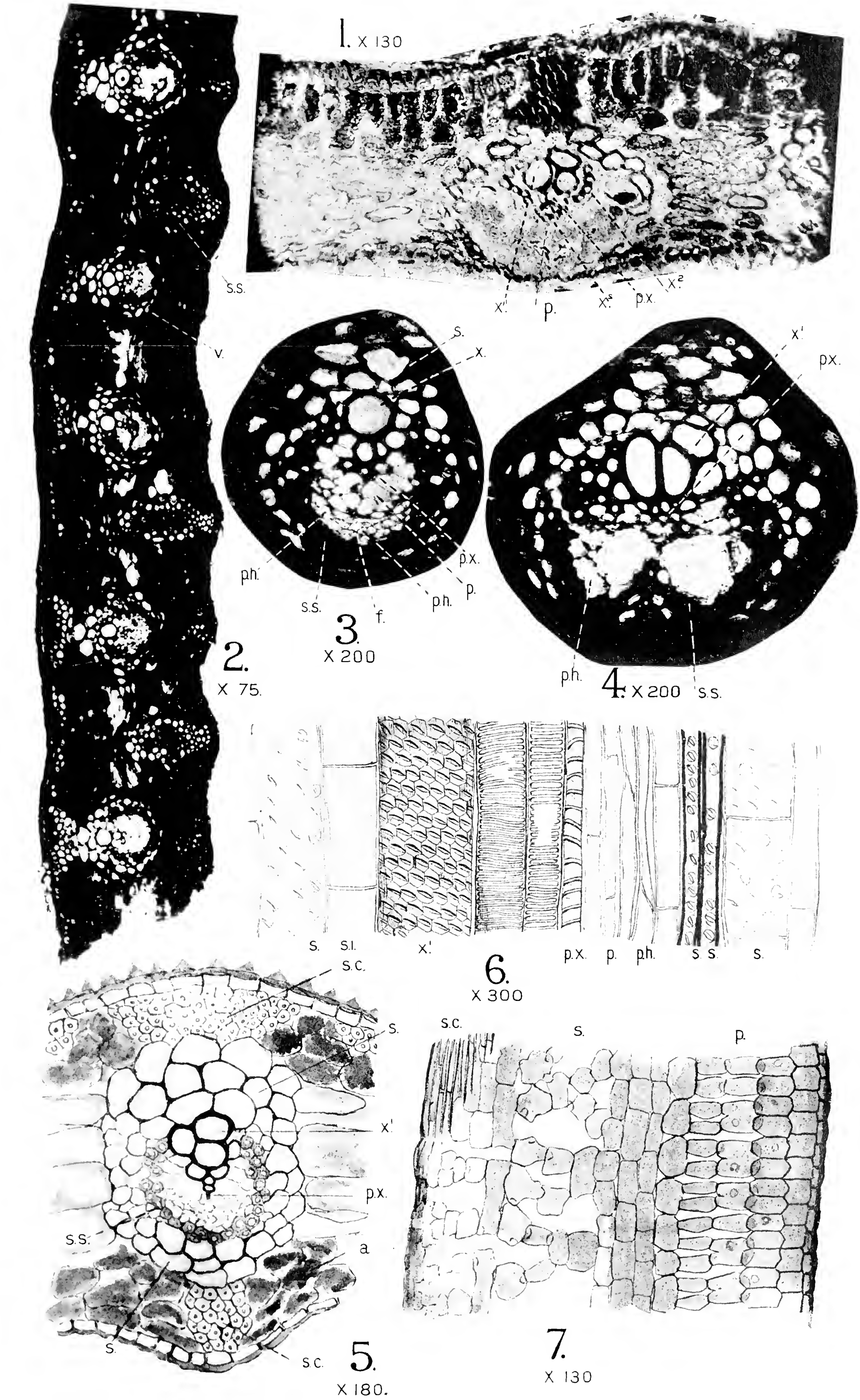
Highley lith. et imp.

Chick-Seedling of Torreya.



E.C del.

CHICK—SEEDLING OF *TORREYA*.



W. Tams, Photo
M. S., Del.

STOPES _ LEAF OF CORDAITES.

Bemrose Ltd London, Derby & Watford.

bases his species. The exact size of the leaf is not mentioned by him, but working from his figures we find it corresponds to ours, *i.e.*, ·4 mm. in thickness; as also does the distance between the bundles, both Renault's and ours averaging ·45 mm. The only essential difference is in the presence of centrifugal xylem in Renault's figures, a point which we have already endeavoured to explain. The two leaves in this case coinciding so exactly in all respects, it seems needless to found a new species to receive the one under consideration.

We shew for comparison a cross section of a bundle and adjacent parts of the leaf of *C. lingulatus* (phot 1.) which has undoubted centrifugal xylem; with the phloem, which unfortunately does not show up well, in its proper position outside it.

As a Cordaitean character possibly too much weight may have been attached to the presence of centrifugal xylem in the foliar strand. There are three sets of original figures of structure specimens of Cordaites; the well-known ones of Renault[1], those of Grand' Eury[2], and those of Felix[3]. Of the six species figured by Renault, three only (*C. angulostriatus*, *C. lingulatus*, and *C. principalis*), are described as possessing centrifugal xylem, and if, as we are inclined to suppose, the last is without it, there remain but two. Of Grand' Eury's three examples none shew it, and of Felix's three figures one only shews it clearly, one has cells which might be interpreted in this sense, and one has none. So that on the whole, the majority of known Cordaitean leaves appear to be without centrifugal xylem.

Hence there seems to be some resemblance between the leaf bundles of most species of *Cordaites* and the petiolar bundles of *Medullosa* which, as is well-known, are exarch. They are of somewhat simpler type in *Myeloxylon radiatum* (the petiole of a *Medullosa*), the xylem consisting only of spiral and finely reticulate tracheides, the large pitted elements found in *Cordaites* and *Cycas* not being represented; the sheath also is simpler and is composed of fibres differing in no important respect from those surrounding the mucilage ducts, and hence having no affinity with transfusion-tissue.

[1] Renault, Structure comparée de quelques tiges de la Flore Carbonifère, pl 16. Cours de Bot. fossile I., plate 12. These are the same figures.

[2] Grand' Eury, Flore carbonifère de Dépt. de la Loire et du Centre de la France, pl. xviii., and Geol. du Gard.

[3] Felix, Untersuch. über den innern Bau Westfälisches Carbon planzen, plate iii.

This type of bundle is also found at the edges of the leaves of *Poroxylon*[1] which are described as lacking the centrifugal wood of the main bundles. The modern Cycads on the other hand shew a parallel to the more complicated type of the Cordaiteae in which, as in *C. lingulatus*, the centrifugal xylem is well developed.

I am much indebted to Professor F. W. Oliver for the use of the fossil slides, and for the interest he has shewn in their description. The sections figured are all in the collection belonging to the Botanical Department of University College.

[1] Bertrand and Renault, Recher. sur les Poroxylons, p. 354.

EXPLANATION OF PHOTOGRAPHS AND FIGURES ON PLATE IX ILLUSTRATING MISS M. STOPES' PAPER ON "THE LEAF STRUCTURE OF *CORDAITES*.

Photograph 1.—Trans. sect. of the leaf of *Cordaites lingulatus* (× 130.)

px. protoxylem
x^1. centripetal xylem.
x^2. centrifugal xylem.
p. phloem.

Photograph 2.—(et seq). *C. principalis*. Trans. sect. of leaf (× 75.)

v. vascular bundle.
s. large sclerotic strand on the lower side.

For details see photos. 3 and 4.

Photograph 3.—Single bundle enlarged (× 200). The one nearest the broken end of leaf, phot. 2.

px. protoxylem.
x^1. centripetal xylem.
p. xylem parenchyma.
ph. phloem.
ss. inner pitted sheath (" primitive transfusion-tissue ").
s. outer pitted sheath (" peridesmic transfusion-tissue ").
f. crushed phloem cells, which appear somewhat like xylem as they are out of focus.

Photograph 4.—Bundle about to divide (× 200).

From another bundle of the leaf partly shewn in phot. 2. The inner sheath is beginning to grow in, separating the two groups of phloem.

Figure 5.—Diagram of trans. sect. of a single bundle and adjacent tissues (× 180.)

Lettering as phot. 3.

Figure 6.—Diagram of long. sect. of bundle (× 300.)

Lettering as above.

si. sheath cells adjacent to and above centripetal xylem (? pitted.)

Figure 7.—Parenchyma of leaf (× 130), section cut parallel to midrib and at right angles to plane of leaf, somewhat oblique.

sc. sclerenchyma of large strand on the lower side.
s. spongy tissue.
p. palisade tissue.

OBSERVATIONS ON THE POLLINATION OF THE PRIMROSE,

By F. E. Weiss, D.Sc.

A considerable amount of uncertainty exists as to the manner in which the pollination of the primrose is effected. Darwin[1] has recorded how rarely insects can be seen during the day visiting the flowers of the primrose, and he came to the conclusion that they were commonly fertilized by nocturnal Lepidoptera. Writing in 1897 on the fertilization of spring flowers on the Yorkshire coast Mr. Burkill[2] says with regard to the primrose: "the fertilization of this plant is yet unexplained. None of the insects seen on it through many hours of watching are sufficient for its fertilization." He was consequently inclined to accept Darwin's conclusion as the correct one. In a more recent publication entitled "The Primrose and Darwinism" the author, "A Field Naturalist" states it as his belief "that the primrose gives unimpeachable evidence that self fertilization of heterostyled plants is the natural and legitimate fertilization as being fully productive." This conclusion so directly at variance with Darwin's explanations of the importance of heterostyly as ensuring cross pollination was largely based on the absence of insect visitors to the primrose, of such insects at least as could effect the pollination of the flowers. Only four such visitors were observed by "Field Naturalist," "after seeing and examining thousand and thousands, we might say millions of the flowers."

Other British botanists[3], it is true, have recorded the visits of various insects to the flowers of the primrose, but their observations do not seem to have been regarded as conclusive by Darwin, Burkill, or "Field Naturalist." Knuth[4] has given a complete summary of the observations made upon this subject up to the year 1899 both by himself and others, yet one cannot help feeling that there is a considerable amount of conflicting evidence, for while Knuth and Scott Elliot look upon *Bombus hortorum* as one of the most important agents of pollination, Darwin states definitely[5] that

[1] Darwin, C. Forms of Flowers, p. 36.
[2] Burkill, I. H. Journal of Botany, 1897.
[3] (i.) Briggs. T. R. Archer. Journal of the Plymouth Institution, 1871-72.
(ii.) Miller-Christy. Trans. Essex Field Club, 1884.
(iii). Scott-Elliot. Flora of Dumfriesshire, 1896.
[4] Knuth, P. Blüthenbiologie, 1899, vol. II., p. 313.
[5] Darwin, l.c. page 56.

"the primrose is never visited (and I speak after many years' observation) by the larger humble bees and rarely by the smaller kinds."

These conflicting views do not of course imply inaccurate observations, but may be readily explained by the fact that the latter were made in different localities and, probably, under varying conditions. As I had an opportunity during the Easter vacation of observing large quantities of primroses near Church Stretton in Shropshire, it seemed to me important to make some more observations on the visits of insects to these plants with a view of helping to settle this somewhat vexed question. I confined my observations mainly to two large patches of primroses, on the east and west of a narrow lane a portion of Watling Street. Both positions were sheltered from the prevalent north-westerly winds, which were often strong and sometimes bitterly cold. I visited one or both of these places on eight successive days between 11 a.m. and 1 p.m., staying from half-an-hour to an hour on each occasion, and each time I was able to observe some insects visiting the flowers. Taking the eight occasions together the flowers at these two places were visited by

17 *Bombylius major* L.,
3 *Bombus terrestris* L.,
7 *Anthophora furcata* P_z (6 ♀ and 1 ♂),
1 *Apis mellifica* L.,

and by numerous (more than 20) *Andrena Gwynana* K.

On two occasions observations were made on two other stations and yielded

3 *Bombylius*,
4 *Bombus*,
5 *Anthophora*,
2 *Apis*,
numerous Andrenas.

The number of insects varied greatly on different days, owing to considerable differences in the temperature, and to different amounts of sunshine.

It will be noted that *Bombylius* was the most frequent of the long tongued insects, and was a far more regular visitor than the Andrenae, which, though present in considerable numbers on the 19th and 20th of April when the sun was powerful and the wind less strong, were absent during the earlier days, when there was less sun and a stronger wind. *Bombylius*, indeed, was the most

regular of all the visitors, having been observed on seven days out of the eight, and on the occasion when he was not observed I think this was due to my visit being earlier than usual, *i.e.* before 11 a.m. A fresh wind from the north-west was blowing at the time and very few insects of any kind were to be seen, so that in all probability *Bombylius* would have made its appearance a little later in the morning.

Bombylius, as has been noticed by other observers, hovers about the flowers in the graceful manner of a humming bird or humming bird hawk-moth and is said by some not to settle on the flower. Though this may be the case with certain flowers, yet in almost every instance when it visited the primrose, I saw this graceful insect ultimately settle on the flower, and, after its wings had come to rest, push its head as far as possible down the corolla-tube and remain in that position for some time, evidently sucking nectar. This is no doubt necessitated by the very long corolla-tube of the primrose, and it is an important fact, as the tuft of hairs on the top of the head thereby comes in contact with the pollen of the short-styled forms, and becomes a means of pollinating the long-styled flowers.

After visiting a few primroses (three or four) on the earlier colder days, and as many as eighteen or twenty in warmer weather, *Bombylius* rested on a dead leaf, well protected by its colouring, and cleaned off the pollen grains that were adhering to its head and proboscis. Considering the regularity of the visits of *Bombylius* and the relatively large number observed in really fine weather, eight in an hour and a half on April 19th, I have no doubt that this insect is an active agent in the pollination of the primrose. It seems admirably suited to obtain nectar from the depths of the tubular corolla with its long proboscis, and it seemed at this time of the year to confine its attention to the primrose. Only on one occasion did I observe a *Bombylius* sucking nectar from the celandine which is so largely visited by the ordinary bees.

Various species of *Bombylius* are known to visit other species of Primula, as for instance the Bardfield Oxlip, and even on the primrose Archer Briggs[1] observed *Bombylius medius*, a slightly smaller species, as did also Cobelli,[2] 1892.

As stated above there is a considerable difference of opinion

[1] Briggs, A. l.c.

[2] Cobelli, R. Zool. Bot. Ver. Wien. Abhandl.

as to whether the larger humble bees visit the primrose or not. On five different occasions I have observed *Bombus*, chiefly, I think, *Bombus terrestris* visiting primroses, and generally in such a manner as to ensure the pollination of the flowers. In two cases, however, I noticed the humble bee not sucking at the flower but moving all over the corolla, both at the front and the back of the flower, apparently endeavouring to obtain the honey by illegitimate means, just as Darwin observed them at times biting through the corolla in the case of the cowslip, of which they are regular visitors. I ought to state clearly that *Bombus* was a more frequent and regular visitor of other flowers than the primrose, and was more commonly seen on the willow, the dandelion, the violet, and the barren strawberry.

A smaller humble bee however, *Anthophora furcata*, though less plentiful in the district, was more often seen on the primrose to which it seemed to confine its attention. There can be no doubt that this insect is both able to gather honey from the primrose flower and also to effect its pollination. The female insects were more frequent visitors than the males, from which they differ greatly in appearance, and they seemed to be also more efficient as pollinating agents, as they remained longer at the flowers.

Apis mellifica L appeared to be less hardy than the humble bee or *Bombylius*, for it only gathered honey on warm days and was not observed at all on several days, when *Bombylius*, *Bombus* and *Anthophora* were about.

The bees visited chiefly the celandine, barren strawberry, wood anemone, violet and dandelion. Occasionally a stray one would visit a number of primroses, but did not spend much time on each. They were evidently endeavouring to obtain the nectar, which however, they were unable to reach. They stayed a little longer on the short-styled flowers from which they collected a little pollen. They were obviously not the regular visitors of the flowers though they could no doubt bring about cross fertilization of the long-styled forms.

The crossing of the long-styled flowers would also be effected by the visits of *Andrena Gwynana* ; but this insect must be placed in a different category from the bee, for it is a regular and busy visitor of the primrose and more commonly seen by me on its flowers than on those of other plants. It was only observed towards the close of my visit when the weather was much milder, but then it was present in considerable numbers. It gathered the pollen greedily, and in

getting at it poked its head deep into the mouth of the corolla. It naturally stayed longer in the short-styled flowers, but its movements in the long-styled forms were sufficient to pollinate the protruding stigma. There would seem to be no doubt that in the Church Stretton district these are very active agents of cross-pollination of the primrose, just as Briggs found them to be at Plymouth. They can however only bring about the pollination of the long-styled flowers.

From the instances given above, therefore, there is no doubt in my mind that primroses are efficiently cross-pollinated in the district under observation by *Bombylius*, *Anthophora* and *Andrena* with the addition of occasional, though by no means isolated visits of *Bombus*, the same genera indeed to which Briggs attributes the pollination of the primrose around Plymouth. The absence of these insects during the observations made by Darwin and Burkill must I think be due to their observations having been made in somewhat exposed situations, at all events this seems very probable in the case of Burkill.

On the days on which I observed insects in the sheltered spots which I had selected, I looked in vain for such visitors in large primrose covered areas at the foot of Caer Caradoc, which were exposed to the west winds which prevailed during my visit.

In normal Spring weather the slopes sheltered from the east wind would probably have yielded positive results, and indeed, on one somewhat less windy day several specimens of *Bombus* were noted visiting the primroses here. On that day *Apis* was also in evidence visiting the celandines and wood anemones with which the primroses were associated.

There is no doubt that unfavourable weather is prejudicial to the cross pollination in many places owing to the absence of insects in those localities. That however, cross-pollination in the district under observation must be a pretty general phenomenon is I think borne out by the fact that in most of the patches of primroses I examined I met with one or more specimens of the so-called oxlip, the hybrid between *Primula acaulis* and *P. officinalis*. Both parents were pretty plentiful in the district and generally specimens of both were found near the hybrids. There can, I think, be no doubt that these hybrids owe their origin to cross-pollination by insects, and as the chances of such hybridisation must be somewhat limited in species which differ slightly in their time of flowering, the occurrence of a fair number of hybrids argues a considerable frequency of insect visitors to both parents.

I did not come across any of the beetles *Meligethes pieipes*, (Sturm) which Christy found so frequently on the primroses in Essex; nor was I able to observe any butterflies alighting on primroses, but that may have been due to the scarcity of Lepidoptera owing to the cold weather. No observations were made at night as the severe night frosts seemed to preclude the possibility of nocturnal visitors to the flowers.

Self Pollination.

That self-pollination may occur fairly often in the primrose cannot be denied, and indeed, Darwin observed the frequent presence in both the cowslip and the primrose of Thrips which he considered aided the self fertilization of both forms.[1] In many primroses which I examined numbers of Thrips were present and in these flowers it was very common to find pollen grains scattered throughout the tube of the corolla and it seemed likely that it had been carried about there by these small insects.

Another agency for self-pollination is no doubt the wind taken in conjunction with alterations in the position of the flower. I agree with "Field Naturalist" in thinking that too little importance was attached by Darwin to the effect of the wind. At all events in the absence of cross-pollination which must frequently happen in flowering plants, in early spring the strong winds of that season are probably of considerable use. Watching the primroses on the hill-side, much exposed to the wind and in which the absence of insects as stated above was very marked, the violent shaking of the flowers was a noticeable feature.

This must however be considered in conjunction with the singular adaptation for self pollination which I think is shown in both the primrose and the cowslip, in the changes in position of the flower. In the primrose the flowers open at first in a vertical position and if the flower is short-styled the pollen from the opening anthers can readily be shaken by the wind on to the lower standing stigma. But towards the end of the flowering the flower stalk has grown considerably in length and the flower passes into a horizontal and often a pendant position so that the long-styled forms have a chance of self pollination too, when the flowers are agitated by the wind. It may be thought that this movement is mainly for the concealment of the fruits which in the primrose are ripened beneath the foliage, but though this may be to a certain extent the case, I cannot but believe that the self-pollination is also a

[1] Darwin., l.c., p. 37.

determining factor in this movement. For in the cowslip the very opposite occurs. The flowers, at first pendant, offer greater facilities as far as self-pollination is concerned to the long-styled forms, but later on the flowers become erect and thus in the absence of cross-pollination the short-styled forms will have ample opportunity to be self-pollinated.

From the observations I have made on the primrose I feel convinced that it is both regularly visited and cross-pollinated by insects under favourable climatic conditions, but that like most flowers adapted to the visits of insects, it is provided with efficient means for self-pollination and these are important to a plant flowering at so early a period of the year when the visits of insects may be precarious.

ON A NEW METHOD FOR FACILITATING THE STAINING OF MICROSCOPICALLY SMALL OBJECTS,

By V. H. Blackman, M.A.

THERE is a great need for a really satisfactory method of dealing with microscopically small objects so that they can be stained by the most modern methods and handled as easily as are microtome sections fixed to a slide.

The obvious method, by *decantation*, in which the objects (small unicellular organisms, etc.) are fixed, washed and stained by successive quantities of fluid which are decanted off from the sediment of material, is objectionable, not only from its tediousness and difficulty of thorough washing, but also from the fact that it prohibits the use of the more delicate cytological stains. With these stains it is very generally necessary that a given fluid, after producing the right degree of differentiation, should be quickly and completely removed; such a rapid change of fluid is however impossible by the decantation method.

The difficulty in question could clearly be got over by fixing the objects to a slide in the manner of sections. For this purpose two methods have been devised, but both have considerable objections. One method is that of Overton (Zeit f. wiss. Mikrospie Bd. vii. 1890, p. 9), in which the objects, after being brought up to absolute alcohol (if necessary, by placing them in dilute alcohol

in an atmosphere of alcohol), are fixed to the slide by means of a thin film of celloidin. The objections to this method are, that though it allows of a rapid transference from one fluid to another, yet the presence of the film, not only introduces difficulty of clearing, but also prohibits the use of ceitain stains which colour the celloidin too deeply.

A considerable step in advance was made by the "Stippling" method of Harper and Fairchild (Trans. Wisconsin Acad. of Sc., Vol. XII., p 479) in which the fixing fluid together with the objects is "stippled" in drops by means of a fine pipette, upon the surface of a slide prepared with Mayer's albumen fixative. The fixing fluid partly coagulates the albumen and the coagulation is completed by passing through increasing strengths of alcohol, so that the objects remain firmly fixed to the slide. This method is exceedingly ingenious, but is difficult to carry out, is applicable only to very small objects, and, as Harper states, a large proportion of the material is lost in the process. The method now to be described is applicable to both small and large objects (*e.g.* large Desmids and large teleutospores) and when carefully used all the material placed upon the slide is held fast. Historically it would appear to be a modification of the Harper and Fairchild process, but it was actually arrived at by a consideration of the condition of affairs when one melts the paraffin of a microtome section which is lying upon a layer of albumen fixative.

The material to be treated is brought up by decantation, filtration, etc., if necessary, veiy gradually, to some clearing fluid (xylol, cedar-wood oil, bergamot oil, &c.). Drops of the clearing fluid containing the objects are then placed upon tbe surface of a slide prepared with egg-albumen; either in fairly large drops or the "stippling" process can be used, according to the closeness of the objects in the fluid. The drops spread out, but the objects are retained by the albumen. When the fixing fluid has evaporated and spread out to a very thin layer, the slide is placed slightly obliquely, and absolute alcohol is allowed to flow very slowly from a pipette over the surface of the slide. The clearing fluid is washed away, but the objects are retained in position by the sticky albumen, which, being immediately coagulated by the alcohol, holds the material fast. The slide can then be treated in the same way as one to which microtome sections have been fixed. Of the clearing

[1] Harper states that the method can be made applicable to larger objects by washing away the fixative with fairly strong alcohol, but in my hands this has led to collapse of the cells.

fluids xylol is found to be rather too volatile to be easy of use, a mixture of equal parts of xylol and cedar-wood oil works, perhaps, most easily. If cedar-wood oil is used, the objects can very conveniently be brought up to this fluid by placing them in a 10% solution of cedar-oil in absolute alcohol, over calcium chloride in a dessicator. The spreading out of the drops of cedar-wood oil on the slide should be accelerated by warming on the paraffin oven.

The method is, of course, a much longer one than that of Harper and Fairchild, as the objects have to be brought up to a clearing fluid before they can be placed on the slide, but it has the advantages of being easily applicable to both large and small objects and of involving no loss of material in the process of fixing to the slide. Moreover, the method can obviously be applied to material which has been fixed in any way. It is useful, among other purposes, in making slides of *plankton* material, and even with ready stained material which only requires mounting in balsam, I have found it convenient to mount on a thin layer of albumen; by this means one avoids the shifting of the objects likely to be caused by the addition of balsam or of the cover-slip.

ON DESCRIPTIONS OF VASCULAR STRUCTURES.

IN describing the course of the vascular tissues in the stem, it is more convenient in some cases to trace them in the acropetal direction, in other cases in the reverse order.

De Bary,[1] speaking of "common bundles" (*i.e.* those belonging to stem and leaf), writes as follows. "Their course in the stem is most clearly understood by following them from their point of exit in a basipetal direction, that is downwards. The description of their course in this direction also corresponds best to the facts, inasmuch as at least in most cases the development of the common bundles begins at the point of exit, and proceeds on the one hand towards the leaf, and on the other downwards in the stem." For example one may speak of a leaf-trace as passing[2] through the cortex of the stem into the bundle-ring and then downwards through so many internodes before fusing with the leaf-trace of a certain

[1] De Bary: Comparative Anatomy, English Edition, p. 234.

[2] The metaphorical use of words signifying motion, in the same manner as they would be employed for describing the course of a road, avoids a lengthy periphrasis.

other leaf. In the case of the stem of a typical Dicotyledon, in which all the primary bundles are leaf-traces, the above method of description is no doubt the most convenient.

When one is dealing with certain ferns, which have a solid cauline stele, or in which there are no leaf-traces showing distinct individuality in the internode, often the easiest method of description is one, which starts with the internodal structure of the stele and follows the acropetal direction to the node; in this way it is clearly seen what part of the stele is continuous with the leaf-trace. The acropetal order has been largely followed in recent papers on ferns, when the authors have been dealing with the structure of the mature stem, and is naturally adopted in the fern-seedling, when the object is to trace the gradually increasing complexity in the arrangement of the vascular tissues of the stem as shown by the ontogeny.

In many cases, according as one describes the vascular and other tissues as traced upwards or downwards, one is easily led to use phrases, which commit one to a different opinion as to their morphological nature in the two cases. To take an example, in certain species of *Gleichenia*, *e.g.* *G. flabellata*[1] the internodal structure shows a stele with a central solid mass of xylem (*i.e.* a protostele); as one approaches the node from below, a strand of sclerotic tissue appears in the xylem[2], but, at the node, becomes connected with the sclerotic tissue of the cortex, during the separation of the leaf-trace. Firstly, adopting the acropetal order, one states that a strand of sclerotic tissue appears in the xylem of the stele and becomes continuous with the cortex at the node. Secondly, the opposite treatment is to describe a strand of sclerotic *cortex* as penetrating the stele at the node and passing downwards for a short distance within the stele. According to the method pursued one is led to regard this strand as belonging to the stele in the one case and to the cortex in the other.

As a second example we will now take the young sporophyte of a fern, such as *Anemia Phyllitidis*, the mature stem of which is dictyostelic[3], that is to say its vascular tissue forms a tubular network of concentric vascular strands. The lower part of the seedling-stem has a simple stele containing a centrally placed solid core of xylem. In passing upwards, the middle part of the xylem

[1] See Poirault, Recherches sur les Cryp. Vasc., Ann. des Sci. Nat., Bot, 7 sér, tom. xviii., p. 177, Fig. 17 and Boodle, Anatomy of the Gleicheniaceae, Annals of Botany, vol. xv., p. 1-23.

[2] Further details are omitted for the sake of clearness.

[3] Brebner, Anatomy of *Danaea*, etc., Annals of Botany, vol. xvi., p. 523.

becomes replaced by other tissues—ultimately by central parenchyma bounded externally by endodermis, between which and the (now annular) xylem there is a ring of phloem; at the nodes the central parenchyma becomes continuous with the cortex through the leaf-gaps, which finally become crowded, so that, at any succeeding level, the central tissue and the cortex are connected at more than one point. This mode of description may be taken to imply that the central tissues within the xylem-ring of the seedling belong to the stele. Whereas, if we trace the series in the reverse order, we start with vascular strands arranged in a ring and separated from one another by leaf-gaps; the cortex is similar to the central parenchymatous tissue and continuous with it, and the two would naturally be described as parts of one tissue (cortex or ground-tissue). Hence the downward continuation of the centrally placed parenchyma, which we find lower down within the closed vascular ring (and internal to an endodermis) we should continue to designate as cortex or ground-tissue, not as part of the stele.

Thus our opinion of the morphological nature of this tissue, *i.e.*, as to whether it represents stelar tissue or cortex, may be first suggested simply by appearances, which differ according to the direction chosen for tracing the tissues, and apart from any further reasoning. In these provisional opinions our view is essentially based on the position of the tissue, if one follows the acropetal order, and on its continuity with and structural similarity to the cortex[1], if one adopts basipetal sequence.

For purely descriptive purposes tissues may be traced upwards or downwards, according as the one or the other method is found to be more convenient for each individual case, but it has to be borne in mind that, if any claim to morphological treatment is intended, the phylogenetic history of the tissues concerned must be enquired into, and either a separate theoretical statement with regard to their morphology must be made, or the topographical statement must be re-worded according to the view arrived at as to the first origin of these tissues.

The difficulty in obtaining a criterion of the morphological

[1] Continuity and structural identity have sometimes been treated as proving morphological identity. This cannot be accepted, but the different parts of the protostele are here assumed to have the same morphological value, and the same is supposed for the different *vascular* parts of the dictyostele, because a continuous conducting system has no doubt been retained constantly throughout the stem.

nature of internal tissues has been pointed out by Farmer and Hill.[1] The subject has not been advanced by treating unproved criteria, such as continuity and similarity of tissues or the endodermal boundary, as final tests of morphology, nor by choosing a morphological unit and applying it in an arbitrary manner. The morphology of vascular tissues at present rests chiefly on *general* theoretical considerations, so that what is required is the careful working out of further morphological test-cases, if satisfactory ones can be obtained, and of phylogenetic series, to provide a firmer basis for the theories afloat. As there is rather a lack of such data, we will only discuss in a general way the probable mode of differentiation of some of the vascular tissues.

The importance of studying the stele in relation to the leaf-gaps has been insisted on by Jeffrey[2] and Gwynne-Vaughan[3], and the vascular structure of the stem is admitted to have been largely modified in relation to the leaf-traces. Further it is certainly probable that many changes, in the direction of complication in stem-structure, began at the nodes and were afterwards continued down through the internodes.

The protostele was probably the type of vascular structure possessed by the stem of the more primitive ferns, and may be taken as a morphological unit, possibly only a rough one (that is to say in a given phylogenetic series the outer limit of the stele may perhaps not remain constant). In the protostele the centrally placed xylem is generally composed of both tracheides and parenchyma (*e.g.* in *Gleichenia*). Such parenchyma may be localised, as in some Hymenophyllaceae (*e.g. Hymenophyllum scabrum*), where it would be called pith, if it were not that protoxylem is differentiated at the centre of it. In *Hymenophyllum* it may be taken for granted that the sub-central group of parenchyma arose either by multiplication of such parenchyma as is usually present in the xylem of a protostele or by the replacement of a certain number of tracheides by parenchyma. The same would apply to such adventitious medullate roots, as are found in many Monocotyledons, where increased diameter of the root is connected with their mechanical function as props. Here again the pith is probably due to the gradual multiplication of a few parenchymatous

[1] Farmer and Hill. Arrangement and Structure of Vascular Strands in *Angiopteris evecta*, Annals of Botany, vol. xvi., p. 393.

[2] Jeffrey. The morphology of the Central Cylinder (1900). Reprint from Trans. Canadian Inst.

[3] Gwynne-Vaughan. On *Loxsoma*, Annals of Botany, vol. xv.

cells (originally xylem-parenchyma or parenchyma derived from potential tracheides), and there is no question of the intrusion of cortex, as there are no leaf-gaps.

The necessity for the supply of a definite amount of water to the leaf-traces, as a function of the xylem of the protostele, appears in combination with other factors to have regulated the mode of differentiation of the latter tissue, and does not directly affect the cortex. Hence, as portions of xylem are easily replaced by parenchyma, it certainly appears more probable[1] that the protostele itself should have become converted into vascular and parenchymatous portions than that an intrusion of cortex into the stele should have taken place. Granting this, the dictyostele together with the parenchyma at its centre and that forming the leaf-gaps may be regarded as the morphological equivalent of the protostele[2].

It may be urged that a probable morphology based on considerations of this kind is of no importance, but many things require investigation before we can hope for a firm foundation for the morphological treatment of vascular tissues, and what is at present important is that one should not build up a spurious morphology with no basis at all, or without stating its basis.

Having discussed some points connected with the morphology of vascular tissues, we may now return to the subject with which we started, and enquire how far the two methods of description (upward and downward sequence) fall in with the theory stated above. We will assume the morphological views, just stated, as correct and also the theory suggested above, that many advances in complexity originated at the node, and spread afterwards downwards through the internode. On these suppositions, both in the seedling and in a mature stem such as that of some *Gleichenias*, in which the structure is not uniform throughout the internode, the acropetal method of describing the tissues gives one their morphology, tissues within the stele being taken as belonging to the stele; while tracing the tissue downwards leads more to a description of the phylogenetic history of the tissues expressed in physiological terms, *e.g.*, in the case of *Gleichenia* referred to above, a downward

[1] For the above reasons, and for others, which cannot be quoted here.

[2] Instead of excluding the parenchyma from the stele, as has been done by Farmer and Hill, loc. cit. The view given above in the text is that which has been adopted by Schoute (Die Stelär-Theorie, 1902).

extension of "cortical" sclerenchyma is probably a historical description of this tissue[1].

Lastly we may combine the information derived from the two methods of tracing the tissues, and state that, from the node, there has been a downward progressive modification of a strand of stelar tissue into sclerotic tissue resembling the cortical sclerenchyma.

The examples chosen in the present article are ferns, and the conclusions are intended to refer to ferns. In the Dicotyledons (leaving polystelic forms apart) it is probable that the pith was originally differentiated from the stele, so that its position and the acropetal method in the seedling give its morphology. The effect of the leaf-traces on the stele has been so great, that not only has the vascular part of the stele come to consist of strands similar to the original leaf–traces, which crossed the cortex (from leaf-base to stele), but the differentiation in the individual strands has in many cases come to be basipetal, as stated by De Bary.

L. A. BOODLE.

[1] In such a case there would be no clue to reduction, if such had taken place, but the description would very probably picture the original development of the structure (see Boodle, Gleicheniaceae p.p. 737-738.)

MYCOLOGICAL NOTES.

The Origin of the Ascomycetes.

THE question of the origin of the Ascomycetes has always been one of great interest, so that during the last twenty-five years, as our knowledge has increased step by step, the views put forward have been very various. There is the older view of De Bary that the Ascomycetes are related to the Oomycetes, especially to forms like the Peronosporaceae. This idea was mainly based on the similarity of the antheridium and oogonium of the latter group to the structures termed antheridium and ascogonium (oogonium) which are found in such forms as *Sphaerotheca* and *Pyronema* among the Ascomycetes. In De Bary's time there was no direct evidence that any of the Ascomycetes possessed a true sexual process, but the form and relation of the antheridium and ascogonium seemed to point clearly to their sexual nature, although the evidence of actual transference of material from one to the other was wanting.

Some years later, Brefeld—owing to want of direct evidence as to the nature of the nominal sexual organs when present, and to their apparent absence in the higher forms—was led to put forward the view, which held sway for some time, that the Ascomycetes were a group entirely wanting in sexuality. He derived the Ascomycetes from the Zygomycetes, believing that the ascus was nothing more than a sporangium, like that of the Mucorini, which had become definite in form, size, and the number of spores it produced. From later researches it soon, however, became clear that to homologise the ascus and sporangium was a matter of some difficulty. From the observations of Dangeard and others, it became clear that the single nucleus of the young ascus was the product of fusion, usually of two nuclei; it had also been known for some time that the ascospores were produced within the ascus by free cell formation. Both these characters distinguish the typical ascus from the sporangium.

The discovery by Harper, in 1895, of actual fertilisation (*i.e.* nuclear fusion) in *Sphaerotheca*, at once placed the sexuality of the Ascomycetes on a firm footing. This occurrence of undoubted sexuality in such a form would appear to lend great support to De Bary's view of the relation of the Ascomycetes to the Oomycetes. Harper himself, however, was not able to support this idea; a comparison of the cytological characters of the sporangium and ascus had so impressed him with their differences that he was unable to consider them as homologous structures. The question of the ancestry of the Ascomycetes he believed to be a very difficult one, but that, at all events, their relationships should be sought elsewhere than among the Phycomycetes.

The elucidation later of the sexual process in *Pyronema* revealed a new type of fertilisation. Whereas in *Sphaerotheca* the ascogonium was uninucleate and there was only one male nucleus, in the form under consideration both the ascogonium and antheridium contain numerous nuclei and there is a process of multiple fertilisation, numbers of male and female nuclei fusing in pairs within the ascogonium. In so far as the sexual organs were multinucleate, *Pyronema* obviously shewed a closer similarity to the Oomycetes than did *Sphaerotheca*; but so far as was then known, all the Oomycetes possessed uninucleate oospheres. Shortly afterwards, however, Stevens made the interesting discovery that in *Albugo (Cystopus) Bliti* there was also multiple fertilisation; the well-defined oosphere of the usual type

being what Stevens calls "compound" (*i.e.* multinucleate) and fertilised by a large number of male nuclei which pass over from the antheridium. Further studies by Stevens have shown that a series can be traced from the compound oosphere of *A. Bliti* to the ordinary typical uninucleate egg; this has led him to believe that the former is primitive, and that both it and the antheridium have probably been derived from plano-gametangia by the loss of motility of the gametes.

The resemblance between *Albugo* and *Pyronema* is obviously further evidence for the possibility of the common ancestry of Ascomycetes and forms like the Peronosporaceae. It is clear that what is wanted for the elucidation of this question is a thorough study of the simpler, and presumably primitive, Ascomycetes. In this connection Barker (Annals of Botany, Vol. 17, 1903), has lately investigated in detail the development of the ascocarp in *Monascus*, which seems to be a very primitive Ascomycete possessing a simple antheridium and ascogonium, and having, almost without doubt, multiple fertilisation. Barker is led to believe that this type of fertilisation is primitive also for the Ascomycetes, that *Albugo*, *Monascus* and *Pyronema*, are all primitive forms (*Sphaerotheca* being considered as reduced), and that the ancestor of the Ascomycetes is to be sought for in a form like *Albugo*. He would consider the ascogenous hyphae and asci which are produced from the fertilised ascogonium as an interpolated sporophyte generation, comparable with that in *Phytophthora omnivora*, where the oospore on germination produces, not zoospores directly, but a short promycelium on which later a few zoosporangia arise. It is also possible that the ascus can be derived from a zoosporangium in the same way that the ascogonia and antheridia are probably derived (through the Oomycetes) from gametangia; connecting links have, however, yet to be discovered. It is very interesting to note how the most recent work tends to return to De Bary's old view of the relation of Ascomycetes and Phycomycetes, though with the curious extension involved in the belief in the primitiveness of "multiple fertilisation."

V. H. B.

IN a paper published last year in *Postelsia*,[1] K. Yendo points out that owing to the long and irregular coast line of the Japanese islands, a large proportion of their inhabitants are brought into contact with the sea, and hence marine algæ have been utilised for all sorts of economic purposes. Yendo enumerates a number of these seaweeds, and it will perhaps be worth while to draw attention here to a few of the more important.

Laminaria is much used as a food-plant, and in 1894, over 18,000 tons were exported, chiefly to China. The *Laminaria* fishermen wind up the fronds, which sometimes form belts a hundred feet in length and two feet in width, by means of long poles with forks or sickles at the end. Yendo's paper is illustrated by Japanese colour prints, one of which is a most dramatic representation of the Ainu people gathering *Laminaria*.

Porphyra is actually cultivated on a large scale for food! "Slender, bushy twigs are planted in regular rows in shallow and brackish water. Enough space is left between the rows to permit the passage of canoes. Late in winter or early in spring the *Porphyra* plants gather on the twigs." The tiny purple fronds are collected, washed, and dried in layers upon reed mats. They adhere together into a sheet by means of their own gelatine, and these sheets are peeled off the mats, folded and sent to market.

Next to *Laminaria* and *Porphyra* the most useful Japanese alga is *Gelidium corneum*, from which agar-agar is prepared.

Various kinds of *Sargassum* are used as manure, and one species, *S. enerve*, which becomes green on drying, is employed, intertwined with *Laminaria*, in the New Year's day decorations. Yendo says that the plants occupy much the same place in Japanese life that the holly does among the English.

Different species of *Chondrus* and *Gloiopeltis* are boiled up into a kind of laundry starch, and numbers of other seaweeds, are utilised in decoration, or eaten as salads, sauces, etc.

The point to which the employment of algæ has been carried in Japan may be gathered from the fact that Yendo alludes to nearly thirty different species as economically important, although he distinctly excludes from his list those of restricted use.

A. R.

[1] *Postelsia*. The Year Book of the Minnesota Seaside Station, 1901, St. Paul, Minnesota, 1902.

To the Editor of the NEW PHYTOLOGIST.

DEAR SIR,

With reference to my article in the February number of this journal on the subject of the Origin of the Perianth, I have received from Professor K. Goebel, of Munich, an intimation to the effect that I have misrepresented his views on the subject of metamorphosis in flowers by stating that they are both "idealistic" and "resemble Goethe's type-theory." In the first place it must be said that before penning the article I had not read, as I certainly should have done, Professor Goebel's excellent "Treatise on Double Flowers" (1885), a treatise practically exhaustive in the number of interesting and valuable facts it contains. His views on the origin of the perianth are therein, and also in his "Organography of Plants" (the perusal of which I had also stupidly omitted) made plain. On page 276 of the first-mentioned work he says, when treating of the Ranunculacæ: "It cannot be denied that in many cases petals have arisen from meta morphosed stamens. . . . . . But we have no real ground for making this a general rule." Another passage runs thus: "As in this case [Equisetum] certainly in many others, perianth and corolla-formation takes place through transformation of the leaf-rudiments occurring in the neighbourhood of the flower." The calyx he appears to regard with Prantl, as of bracteal origin.

I take this occasion to make every apology to Professor Goebel for introducing his name in connexion with the subject without a discussion of those important views which most directly bear thereon.

But the remarks with which Professor Goebel's name was introduced, had reference to his theory on the morphology of the foliar organs of the flower expressed in an earlier work of his, the "Vergleichende Untersuchungen," and which may be stated thus: "that any foliar organ of a flower, whether sepal, petal, stamen, or carpel, is a modification or transformation of a rudiment, which itself is always of the nature of a *foliage-leaf*." Goebel's view may, in other words, at least, as I understand it, be stated thus: "that the foliage-leaf is the morphological type from which all other kinds of foliar organs are derived modifications." This view, put forward *without any apparent evidence to support or give reason for it*, it is safe, as it appears to me, because correct, to describe as "idealistic." Is it less so than that of Goethe, who merely held that all foliar organs of the plant are modifications of the "leaf," by which he probably meant the foliage leaf? Or, if by type-leaf was meant a purely ideal entity, his view would, in my opinion, be much nearer the truth and might be merely a statement in concrete, though misleading, language of the fact that all foliar organs of the plant are modifications of a primeval ancestral foliar organ now no longer existing, which I for one would be the last to deny. The views of both Goethe and Goebel must be regarded as idealistic for the simple reason that they possess a purely subjective value, being unsupported by the necessary buttress of scientific argument or evidence. On the other hand, Celakovsky's view regarding the ancestral type of the foliar organs, which *is* based on a definite well-thought-out line of scientific argument and theory, is clearly the opposite of idealistic.

In the last (March) number of this journal, (page 66). Dr. Rendle, in a very interesting article on the subject of the origin of the perianth (which I am glad that my own writing should have had the effect of evoking) questions at several points the tenableness of my position. In reference to my statement that sporophylls preceded in time all other kinds of leaves and that the latter must therefore have been derived from the former, the writer says: "this need not imply the derivation of the perianth from sporophylls in the highest group of plants." For "the differentiation of foliage-leaf and sporophyll was an established fact before the evolution of the Angiosperm and there is therefore no *á priori* reason for deriving the floral envelopes in the latter group from sporophylls."

Dr. Rendle here refers to the *direct and immediate* origin of vegetative foliar organs, such as petals and sepals; for the possibility is not excluded that, at any rate, in some cases, the vegetative foliar organs may have taken, as it were, a step backward and become once more approximated to the fertile region of the axis (from which they were originally derived) in the form of a calyx or even of a corolla. As regards flowering plants generally this theory, in view of all the important and striking facts and arguments which have been brought under my notice, appears to possess but little plausibility as compared with the theory I have supported.

Again, the writer finds it "difficult to accept the statement in its entirety" that calyx and corolla have both sprung from the andrœcium, adducing the argument that the most primitive flowers are unisexual and "have presumably not been derived from an hermaphrodite type, yet we find in the female, as well as in the male, instances of a well-defined perianth, which in the case of the female could not have originated from an andrœcium. Hence the origin of perianth from andrœcium cannot have been universal." Now, I fail entirely to see why the most primitive flowers should not *in certain characters* be more advanced and modified than those of plants standing higher in the scale. The complex massing of the flowers in catkins is surely such a highly modified character. So is it also with their striking diclinous arrangements. On the general principle, to which I firmly adhere, that *the undifferentiated must precede in time the differentiated*, and union always precede disunion, it follows that in all departments of the vegetable kingdom, the separation of the sexes must have been a *secondary* process, and hermaphroditism in all cases represent a more primitive state of affairs. Hence it follows that the perianth of a *female* flower could have been quite naturally derived from the stamens in the early hermaphrodite days, and may in some cases represent these stamens in their modified vegetative form. The whole matter is elaborated by Celakovsky in his work on the Flower. As to the case of the glands in the Willow-flower, if these represent a reduced perianth, then they must be regarded as of staminal origin; the fact that they are more numerous in the male than in the female flowers need not necessarily have, either one way or the other, any bearing on the question at issue, being probably due to quite other causes. Nor do I see, in reference to the case of the Betuleae mentioned, why the female should be expected to exhibit necessarily a similarity of arrangement to the male flower; for the hermaphrodite flower might, surely, have become modified *subsequently* to the loss of its andrœcium?

In his discussion as to the relation between the perianth and the bracteoles in the Coryleae and Betuleae, the writer seems almost driven into a corner in his attempt to account for the origin of the perianth in the former group. Finding a correlation in their *protective* function to exist between the bracteoles and the perianth he feels bound to associate the two sets of organs together in their origin, and, discovering the presence of both perianth and bracteoles in the female flowers of the Coryleae, he concludes that "if it is not possible to regard the perianth as a new foliar organ *sui generis* we must seek its origin in additional bracteoles." This mode of origin of the perianth by the intercalation *ex nihilo* of additional foliar organs *between* those already present at different levels of the axis would be, to my mind, a quite unnatural and impossible one. For whence did these extra bracteoles arrive on the scene? Why not recognise the far more natural, and, to my mind, far less forced method of derivation by means of sterilisation of the stamens in the ancestral hermaphrodite flower?

In treating of the Fagaceae, the writer remarks: "In the male flower the numbers in the two series, perianth and andrœcium, vary in the same direction, an increase in the number of perianth-leaves is associated with an increase, not with a decrease, in the number of the stamens." Here he obviously refers to the case, mentioned by him, of *Nothofagus obliqua*, in whose flowers both stamens and perianth-segments exist to the number of 30—40, which is in contrast to other genera, in which they are often only from 4—7 in number. I regard, however, with Celakovsky, such forms as *Nothofagus*, possessing a large number of stamens, as primitive, while the 4—7 stamens and perianth-segments of other genera must be regarded as the result of reduction from the larger number; hence it is clear that in a case such as *Nothofagus* where an increase in the number of perianth-segments obtains, there can be no possible question of an *increase* in the number of stamens; on the contrary, I hold that very considerable *decrease* in their number must have taken place in order to provide the numerous perianth-leaves which are present.

With regard to the Juglandaceæ, Dr. Rendle says: "There is a strong suggestion of homology of perianth and bracteoles, and it is difficult to imagine a different origin for the two sets of leaves." This is precisely my own view, and I may as well here state once for all my firm conviction that *all* foliar organs (even such curious, independent-looking structures as the cup substending the andrœcium in the Poplar) which are in close proximity to the flower, have, within a comparatively recent period, been derived from sporophylls.

Dr. Rendle himself discovers and acknowledges the production of unisexual flowers by abortion of the stamens in the hermaphrodite flowers of the Saurureae. But he remarks that: "Abortion of the stamens . . . never results in the formation of a perianth." *Abortion* of any organ could surely hardly result in anything but its annihilation! And the absence of a perianth is clearly correlated with the development of the bract as a protective structure for the andrœcium and ovary.

In the case of the Ulmaceæ, &c., the difficulty raised may be easily and quite naturally surmounted by assuming, as in the case of Primula, the abortion of an outer whorl of stamens.

Turning now to the point raised in the penultimate paragraph of

Dr. Rendle's paper: I merely regard the petaloid calyx in flowers containing nectaries as being, for the reasons adduced, more primitive than the green calyx *in flowers possessing a coloured corolla* and in these latter *only*. It is, of course, more recent than the early wind-fertilised flowers. I regard the green calyx of the ordinary entomophilous flower of the Dicotyledons, &c., as having probably passed through the petaloid stage.

The "absence of definiteness in the limitation of distinct series" amongst foliar organs arranged along a spiral line on the axis affords to my own mind a good piece of evidence for the common origin of all the said foliar organs, and this, I hold, must lie in the sporophylls.

Finally, I would refer to Celakovsky's works for more detailed illustration, by means of concrete examples, of the process of origin of the perianth of flowers.

And I would add that where, as in the articles of Dr. Rendle and myself, the *points of view* radically differ, it seems unlikely that any amount of discussion will bring about an agreement.

Yours, etc.,

W. C. WORSDELL.

April 12th, 1903.

THE LONDON BOTANICAL SOCIETY.

At the meeting on Tuesday, March 17th, Mr. S. Hastings shewed a long series of extremely successful habit-photographs of British Fungi, many of which were considerably magnified. The greater number were of Agarics and their allies, but there were also several Ascomycetes in the collection. *Geaster* and *Nidularia* (much magnified) were particularly beautiful examples of the photographer's skill. It is to be hoped that Mr. Hastings may see his way to publish a set of these photographs, since they are some of the best we have seen and really good habit-pictures of plants are always valuable.

Professor J. Reynolds Green gave a most interesting and lucid account of his recent work on the Germination of Fatty Seeds. The time is not yet ripe, however, to publish any details of the results.

At the meeting on Tuesday, May 12th, the Secretary, Professor Farmer, gave an account of the work he has been doing, in conjunction with Mr. J. E. S. Moore and Miss Digby, on the cytological features connected with apogamy in fern-prothalli. It has been successfully shewn that the nucleus of one prothallus-cell passes through the cell-wall where it presumably fuses with the nucleus of the neighbouring cell, from which the apogamous growth originates. The number of chromosomes in the nuclei before fusion is roughly forty,

and after the hypothetical fusion, double that number, or about eighty. The great interest and importance of these results, which go to establish that in the case investigated, so-called "apogamy" is associated with a nuclear fusion having the cytological features of a sexual union, need no pointing out. Professor Farmer hopes to clear up the cytological processes connected with apospory in a similar manner.

Mr. W. C. Worsdell gave an account of his observations on the vascular system in Compositae and Umbelliferae, in which he believes he has obtained evidence that the characteristic bundle ring of the stem of Dicotyledons is derived phylogenetically from the scattered arrangement found in most Monocotyledons. Mr. Worsdell considers that the peduncle is more likely than the seedling to present ancestral features in the arrangement of the vascular system. This opinion drew a protest from Miss Ethel Sargant, who pointed out that there was still a very wide divergence in the "canons of criticism" employed by different investigators of the morphology of the vascular system. It is certainly true that the whole subject is still in its infancy, and that a great deal more work has yet to be done before general agreement can be reached as to what is of value in attempting to trace the evolutionary histories of form in the structure of Angiosperms. The *a priori* method is at present quite illegitimate—we know far too little of the facts. In the case of Ferns the problems are decidedly simpler, and we are now within reach of a fairly clear and comprehensive general theory.

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ON ASEXUAL REPRODUCTION AND REGENERATION IN HEPATICAE,

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(WITH EIGHT FIGURES IN THE TEXT).

IT is well known that the Moss-gametophyte possesses in a marked degree the faculty of regeneration, and that almost every part of the plant may, under suitable conditions, give rise to protonemal filaments, from which new plants are developed. In many Mosses, the production of protonema is confined to more or less modified and specialised organs, which previously become detached from the parent plant. Correns has, in his valuable "Untersuchungen,"[1] framed a somewhat elaborate classification of these organs of vegetative propagation. Although various writers have described examples of similar phenomena in the Hepaticae, none has yet collected and summarised the available information on the subject, in the same way that Correns has so ably done in the case of the Mosses. The object of the present paper is to present a resumé of the principal results that have been published up to the present time, together with some new observations.

In many Hepaticae, asexual propagation is brought about by the dying away of the older parts of the shoot from behind and the setting free of the younger parts or branches as independent plants.

In other cases, the plant bears, often in very large numbers, small few-celled bodies (gemmae), which become free and produce new plants. A third method of propagation, not always easy to distinguish from those just mentioned, consists in the separation from the main axis of buds or branches, either normal or adventive in origin. It is sometimes difficult to draw a sharp distinction

[1] Correns, C., Untersuchungen über die Vermehrung der Laubmoose durch Brutorgane und Stecklinge. Jena, 1899.

between a caducous adventive shoot and a gemma, these types being connected by intermediate forms.

It will be convenient to deal first with the methods of propagation which have been actually observed in nature, taking the families of Hepaticae in turn, and afterwards to describe the processes of regeneration observed when the plants are cultivated and experimented with in the laboratory, under various conditions that differ more or less from those under which the plants grow naturally. The two sets of phenomena, which we may distinguish as natural and induced respectively, in some respects coincide, whilst the facts obtained by experiment often throw light on those observed in the field and lead to certain generalisations and conclusions which will be discussed later.

Naturally-Occurring Organs of Asexual Reproduction.

I. *Marchantiales.* In this group, asexual reproduction is chiefly carried on by the dying away of the older parts of the branched ribbon-like thallus and the liberation of the ordinary branches, or by means of adventive branches, though in some cases (*Marchantia*, *Lunularia*, *Fegatella*) specialised gemmae are produced.

Fam. I. *Riccioideae.* Very common in this family is the formation of adventive branches, which arise from the ventral surface of the thallus, ultimately becoming detached. In *Ricciella fluitans*, the sterile form of which occurs floating on water or submerged a little below the surface, the formation of these branches is often so abundant that the plants cover a sheet of water in much the same manner as Duckweed. In *Ricciocarpus natans*, the broad heart-shaped thallus after repeated branching often becomes split longitudinally, each half giving rise to a separate plant. This splitting occurs regularly in fertile plants and results in the rupture of the embedded capsules and the shedding of the spores. In several species of *Riccia* which inhabit dry regions, *e.g.*, *R. vesicata*, *perennis*, *bulbifera*, the plant produces special ventral branches, each of which becomes swollen up terminally and forms a tuber. These tubers, the tissue of which contains reserve food materials, chiefly in the form of oil-drops and proteid grains, are adapted for enduring a dry period, afterwards giving rise to new shoots.

Fam. 2. *Corsinioideae.* In the two genera included here, *Corsinia* and *Boschia*, adventive branches are occasionally formed, as in the Riccioideae.

Fam. 3. *Targionioideae.* *Targionia* is characterised by the constant production of ventral shoots from the sides of the mid-rib. The main axis seldom shows apical branching, its growth in length being usually arrested by the formation of the female receptacle. The ventral shoots become detached at the base and form new plants.

Fam. 4. *Marchantioideae.* In many of the forms belonging here, especially in the section "Operculatae," *e.g.*, *Reboulia*, *Asterella*, apical branching is largely replaced by the formation of ventral shoots which arise near the apex of the thallus or from the sides of the mid-rib farther back. In two Californian species of *Asterella*,[1] viz., *A. Bolanderi*, *A. violacea*, both the antheridia and the archegonia are borne on short latero-ventral branches, and doubtless in these, as in other species, sterile branches arising in this way may become detached and produce new plants. In *Fegatella supradecomposita*,[2] a Japanese form, the growing-point of each of the thallus-lobes frequently gives rise to a circular discoid outgrowth, which bears ventral scales and obviously represents a modified branch. Instead of simply growing out to form a continuation of the main shoot, like the resting branches formed in autumn in *F. conica*, each of these buds or branches in *F. supradecomposita* becomes detached at the base and gives rise to an independent plant. In *F. conica* itself, as was first shown by Karsten,[3] tubers are often formed on the ventral surface of the mid-rib, especially in old plants which have become covered over by the younger shoots. Here and there the cells immediately below the surface grow and divide actively, giving rise to a mass of tissue which later breaks through the superficial layer and projects as a small spherical ovoid outgrowth, attached by a short narrow stalk. This tuber bears rhizoids, its cells contain starch-grains, and it ultimately drops off and grows out to form a new plant. The tubers of *Fegatella*, which grows chiefly beside streams, are not adapted to withstand drought, as are those of the xerophytic *Riccia*-species above mentioned; they perish if kept dry for a few days.

Adventitious shoots have in rare cases been observed to arise from the specialised female branches (archegoniophores) of *Mar-*

[1] Howe, M.A., The Hepaticae and Anthocerotes of California. Mem. Torrey, Bot. Club, Vol. 7, 1899.

[2] Lindberg, S.O., *Sandea* et *Myriorrhynchus* nova Hepaticarum genera. Acta Soc. pro Fauna et Flora Fennica, Vol. 2, 1884, nr. 5; Goebel, Organographie der Pflanzen, p. 274, fig. 174.

[3] Karsten, G., Beiträge zur Kenntniss von *Fegatella conica*. Botan. Zeitung, 1887, p. 650.

chantia[1] and *Dumortiera*,[2] either from the grooves in the stalk or from the sterile lobes between the groups of archegonia.

In *Marchantia* and *Lunularia*, asexual reproduction is extensively carried on by means of specialised organs, the gemmae, produced in crescent-shaped (*Lunularia*) or cup like (*Marchantia*) receptacles on the dorsal surface of the thallus. These gemmae have been described and figured in various text-books and have formed the subject of much interesting physiological work. At the point where a receptacle is about to be formed, the development of the ordinary air-chambers of the thallus ceases for a time and a shallow depression is formed. At the margin of this depression, either only on the side farthest from the growing-point of the thallus (*Lunularia*) or all round (*Marchantia*), the air-chamber tissue grows up to form a ridge, which is in *Marchantia* cut up into numerous long triangular lobes. Each gemma is formed from a single cell, which grows up and first becomes divided by a transverse wall; the upper cell gives rise to the gemma, the lower one remains undivided and forms the short stalk. The gemma remains throughout bilaterally symmetrical[3] and when fully formed consists of an oval disc, several cells thick in the middle and thinning out towards the margin, which shows two lateral notches at opposite points. Between the gemmae there grow out long club-shaped hairs; the mucilage secreted by these hairs swells up on absorbing water and causes the gemmae to be torn from their short stalks, the loosened gemmae then being washed away by rain-drops. Most of the cells of the gemma contain chlorophyll, and scattered through its tissue there are several cells each containing a large oil-body. Certain of the superficial cells, on both sides of the gemma, are distinguished from their neighbours by their large size and dense protoplasmic contents; these cells, which are devoid of chlorophyll, project from the surface of the gemma. When the gemma is sown, whichever of its two surfaces happens to come into contact with the soil, and therefore is farthest from the light, becomes and remains the ventral surface of the young plant. One of the growing-points, situated in the lateral notches of the gemma, becomes the apex of the thallus; sometimes both of these growing-points become active. In the dorsal region

[1] Klein, J., Ueber Sprossung an den Infloreseenzstielen von *Marchantia polymorpha*. Botan. Centralblatt, Band 5, 1881, p. 26.

[2] Lindberg, S. O., Hepaticae in Hibernia mense Julii 1875 lectae. Acta Soc. Sci. Fennicae, Vol. 10, 1875, p. 468.

[3] Pfeffer, W.. Studien über Symmetrie und specifische Wachsthumsursachen. Arb. des botan. Inst., Würzburg, Band 1, 1874, p. 77.

of the young plant, air-spaces are formed, whilst the cells towards the ventral surface remain in close contact with each other, and the large superficial cells mentioned grow out to form rhizoids. The germination of the gemmae has been carefully studied by Pfeffer, Zimmermann,[1] and Benecke.[2]

II. *Jungermanniales.* A. *Jungermanniaceae Anacrogynae.* In the thalloid forms belonging to this series, vegetative reproduction takes place by the same methods as in the majority of the Marchantiales, namely, the separation of the younger branches by the dying away of the older parts of the thallus, and the production of caducous adventive branches. When gemmae are developed, these are usually much simpler in structure than in the Marchantiales.

Fam. 1. *Sphaerocarpoideae.* In *Sphaerocarpus*, adventive branches are frequently formed from various parts of the thallus, arising from the superficial cells and ultimately falling away and growing independently. The tubers of *Geothallus tuberosus*, an interesting Californian liverwort described by Campbell,[3] may be mentioned here, though their function appears to be rather that of enabling the plant to persist during seasons of drought rather than that of bringing about asexual multiplication of the plants. The tuber is formed immediately behind the growing-point of the shoot, its tissue consists of cells with dense proteid contents, and it remains alive after the rest of the plant has become withered up. The growing-point at the anterior end of the tuber ultimately resumes its activity and gives rise to a new shoot.

Fam. 2. *Metzgerioideae.* Most of the species of *Aneura* and *Metzgeria* are distinguished by the frequent formation of adventive branches which become detached and form new plants.[4] In *Aneura*, these branches are usually formed at the margins of the thallus; in *Metzgeria*, they arise chiefly from the lower surface of the mid-rib, but may spring from any part of the thallus, on either the upper or the lower surface. Each of these branches is developed from a single cell; this cell projects from the surface and becomes divided by intersecting walls, cutting out a wedge-shaped ("two-sided") cell, which forms the apical cell of the new shoot.

1 Zimmermann, A., Ueber die Einwirkung des Lichtes auf dem Marchantieenthallus. Arb. des botan. Inst., Würzburg, Band 2.

2 Benecke, W., Ueber die Keimung der Brutknospen von *Lunularia cruciata*. Botan. Zeitung, 1903, Abt. 1, p. 20.

3 Campbell, D. H., The Development of *Geothallus tuberosus*. Annals of Botany, Vol. 10, 1896, pp. 491-510.

4 Goebel, K, Ruckschlagsbildungen und Sprossung bei *Metzgeria*. Flora, 1898, p. 69.

In several species of *Aneura* (*A. multifida*, *pinnatifida*, *palmata*, *pinguis*), there are formed, especially at the tips of the thallus-lobes, large numbers of two-celled gemmae. These gemmae were figured accurately by Hofmeister,[1] but Goebel[2] was the first to call attention to their development, which differs from anything hitherto observed in other Hepaticae, except *Metzgeria*. The writer has carefully followed out the process of gemma-formation in *A multifida* (Fig. 1).

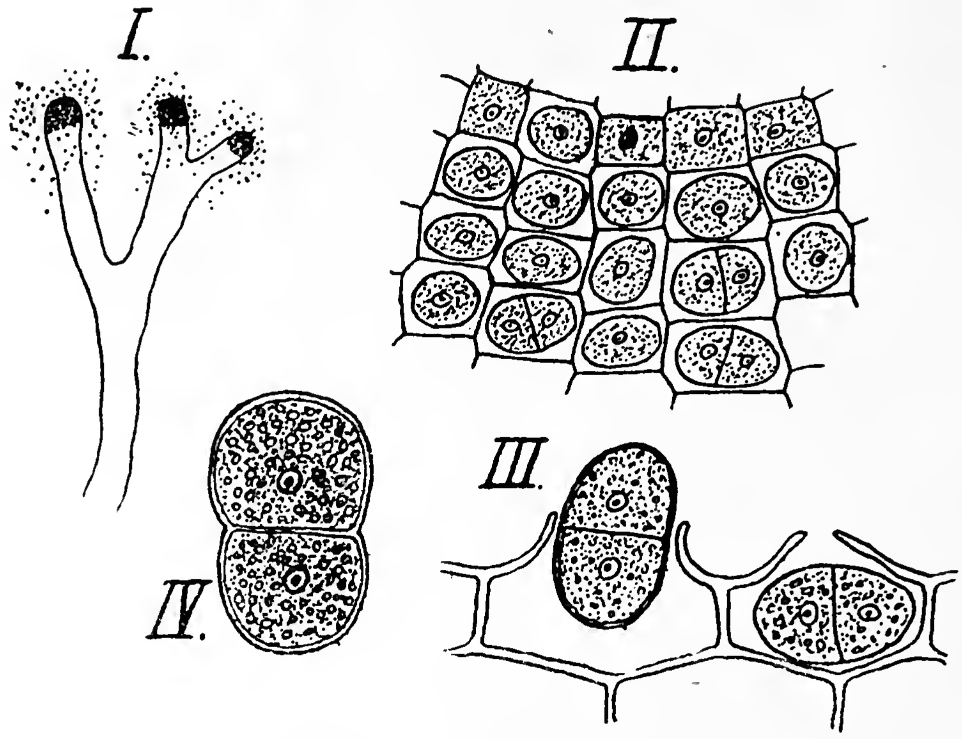

Fig. 1. *Aneura multifida*. I. Part of a plant, showing the ends of the branches covered with gemmae; × 5. II. Cells from the end of a branch. showing stages in formation of gemmae; × 150. III. Two fully-formed gemmae, still within the cells; that on the left is escaping through the pore in the outer cell-wall; × 300. IV. Free gemma, in optical section, showing nuclei and chloroplasts; × 400.

The gemmae are developed endogenously, each being formed within one of the cells of the thallus and escaping by the rupture of the outer cell-wall. The cell-contents contract away from the cell-wall and become covered by a delicate membrane of cellulose. The nucleus then undergoes division; the two daughter-nuclei move towards the opposite ends of the ovoid protoplast, and a median septum is formed. A large portion of the outer wall of the mother-cell becomes absorbed, and the two-celled gemma slips out of the opening thus formed. The gemma contains numerous chloroplasts embedded in dense protoplasm; sometimes starch is also present. The writer has occasionally found that further divisions occur in the gemma before its liberation, so that instead of being two-celled, as is usually the case, the gemma may consist of three or even four cells whilst still enclosed within the mother-cell.

1 Hofmeister, W., Vergleichende Untersuchungen, 1851, Taf. vi., Fig. 29a.

2 Goebel. K., Die Muscineen (Schenck's Handbuch der Botanik, Vol. ii.), 1882, p. 338.

In a tropical epiphytic species of *Metzgeria*, described and figured by Ruge,[1] the thallus bears erect cylindrical outgrowths arising from the dorsal surface of the mid rib. The superficial cells of these erect shoots grow out into discoid gemmae, oval in outline, each gemma being attached by a single stalk-cell and readily becoming detached. In *Metzgeria conjugata*, erect gemmiferou, shoots were observed by Goebel,[2] who states that the gemmae arise in the same manner as those of *Aneura*, but before being set free each gemma has by continued growth and cell-division assumed the form of a concave cell-surface, the "two-sided" apical of the shoot being recognisable on the margin of the discoid gemma. Lett[3] states that in *M. furcata*, var. *aeruginosa* (Hook.), "the fronds mostly bear gemmae in abundance on their ends, and then the branches have their margins so much curved back as to appear cylindrical, and not wider than the nerve."

Fam. 3. *Leptotheceae*. In *Pallavicinia* and *Symphyogyna*, which are included in this small family, and also in *Hymenophyton*, which belongs to the Metzgerioideae, asexual propagation is effected by the formation of ventral branches which arise from the sides of the mid-rib and ultimately become separated from the parent shoot. In these forms, the cylindrical mid-rib of the thallus is traversed by one or more axial strands, the cells of which are long, narrow, pointed at the ends, and bear spirally arranged slit-like pits on their walls. When a branch is laid down, its apical cell for some time produces only broad thin-walled cells, so that the later-formed axial strand of the branch is not continuous with that of the parent shoot, from which the branch readily becomes detached.

Fam. 4. *Codonioideae*. *Pellia* frequently bears adventive shoots, which arise from the superficial cells on the dorsal surface or the margins of the thallus and ultimately become detached. Similar adventive shoots are sometimes observed on the ventral surface of the stem in *Blasia pusilla* and in *Petalophyllum Ralfsii*.[4]

Gemmae occur in three genera belonging here, namely, *Treubia*, *Blasia*, and *Cavicularia*. In *Treubia insignis*, a large foliose form

[1] Ruge, G., Beiträge zur Kenntniss der Vegetationsorgane der Lebermoose. Flora, 1893, Heft. 4, p. 30 of reprint.

[2] Goebel, K., Organographie der Pflanzen, p. 275.

[3] Lett, H. W., A list, with descriptive notes, of all the species of Hepatics hitherto found in the British Islands, 1902, p. 21.

[4] For material of this interesting and rare form, the writer is indebted to the kindness of Mr. W. H. Pearson.

discovered by Goebel[1] in Java, the gemmae, each of which consists of from two to four cells and is borne on a short stalk, are formed from the superficial cells of the stem. In *Blasia* and *Cavicularia*, the gemmae are larger and are produced in large numbers in special receptacles.

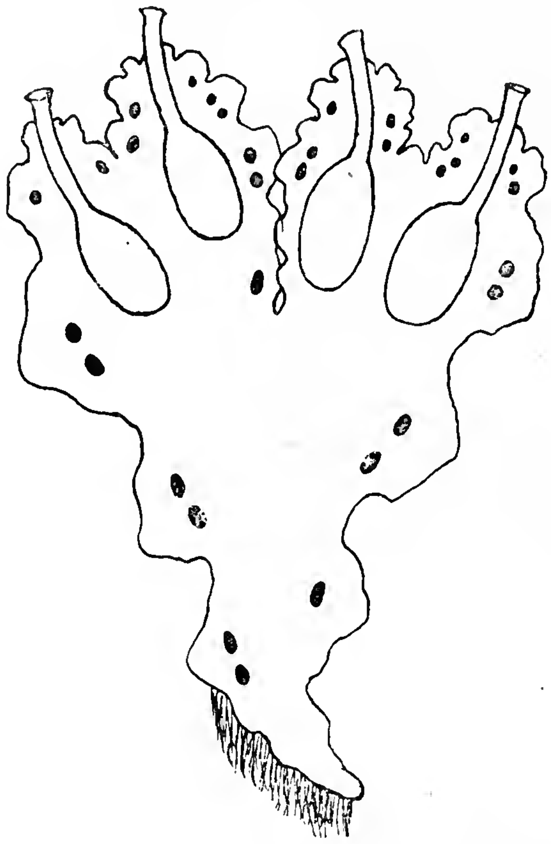

Fig. 2. *Blasia pusilla.* Dorsal view of plant bearing four flask-shaped gemma-receptacles, each with a long tubular neck; the darkly shaded patches represent the *Nostoc*-cavities, two of which are usually found at the base of each of the broad lateral lobes or leaves. × 5.

In *Blasia pusilla* (Fig. 2), the shoot consists of a broad stem bearing on either side a series of oval leaves which lie in the same

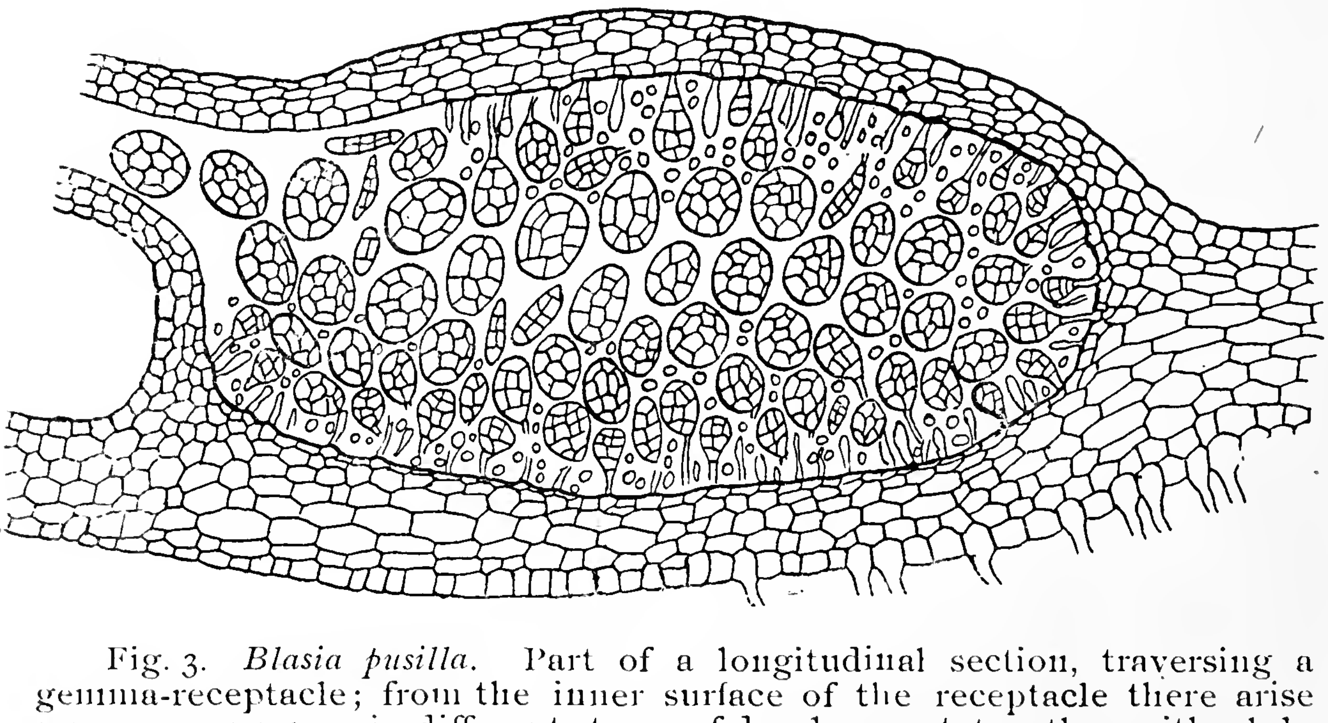

Fig. 3. *Blasia pusilla.* Part of a longitudinal section, traversing a gemma-receptacle; from the inner surface of the receptacle there arise numerous gemmae in different stages of development, together with club-shaped mucilage-hairs. × 60.

[1] Goebel, K., Ueber Javanische Lebermoose. I. *Treubia insignis*, Annales du jardin botanique de Buitenzorg, Tome 9, 1890, p. 1.

plane as the stem and consist for the most part of a single layer of cells (Fig. 4, L.). The upper surface of the stem sometimes bears here and there scale-like outgrowths, somewhat resembling the ventral scales (amphigastria) found in two rows on the ventral surface. These dorsal outgrowths may be regarded as discoid gemmae, as they ultimately become detached and give rise to new plants.[1] Gemmae of a different kind and much smaller size are produced within flask-shaped receptacles, each of which stands

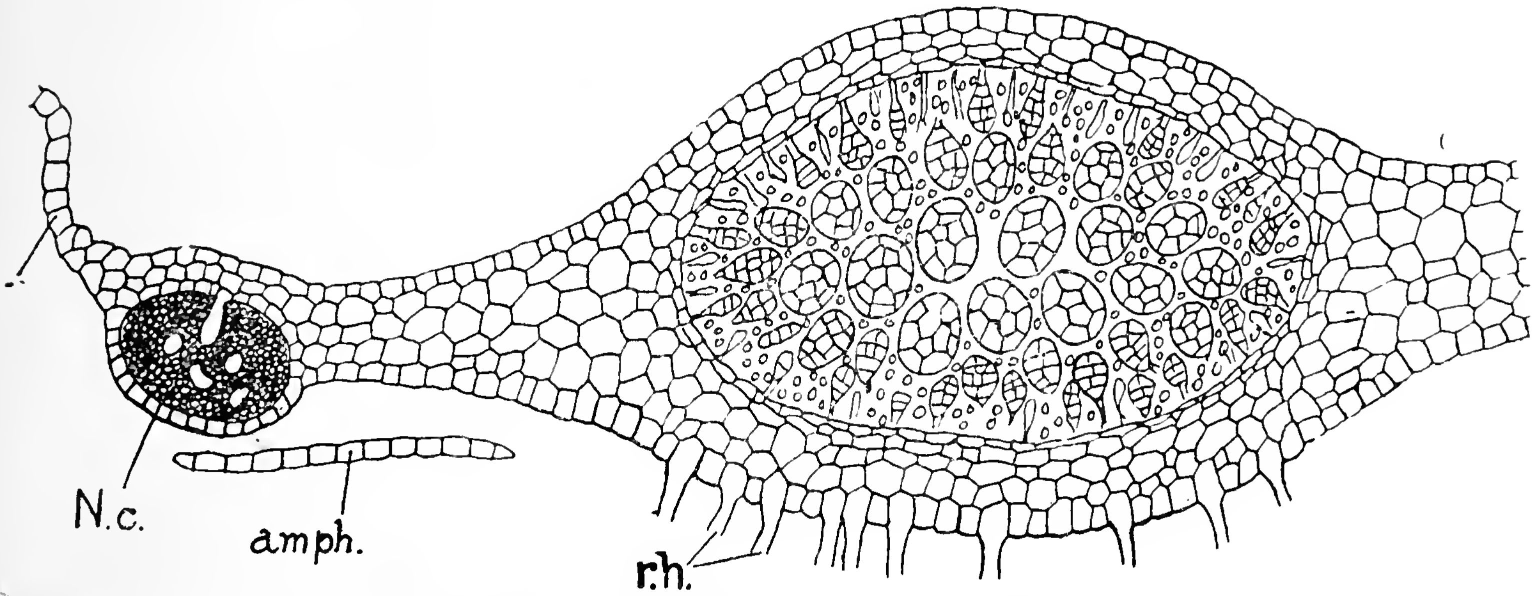

Fig. 4. *Blasia pusilla.* Part of a transverse section, traversing a gemma-receptacle and a *Nostoc*-cavity (*N.c.*); *L.*, leaf; *amph.*, amphigastrium or ventral scale; *rh.*, rhizoids. × 60.

near the growing end of a branch and consists of an ovoid basal portion and a long tubular neck. The neck projects forwards and ends in a trumpet-shaped mouth; its wall is from two to four cells in thickness. The gemmae are produced on nearly the whole of the inner surface of the receptacle (Figs. 3, 4), each gemma consisting of an ovoid or spherical mass of cells, about 0·14 mm. in maximum diameter, borne on a slender stalk about 0·3 mm. in length when the gemma is mature. Between the gemmae there arise numerous club-shaped glandular hairs, the mucilage secreted by which swells up on absorbing water and is forced out through the long neck of the receptacle, carrying with it the gemmae, which have been torn from their stalks.

In *Cavicularia densa*, an interesting Japanese form,[2] the gemmae are borne in crescent-shaped receptacles, resembling those of *Lunularia*. Two kinds of gemmae are produced, either in the same or in separate receptacles. Some of the gemmae are lens-shaped, resembling those of *Marchantia* and *Lunularia* in having

[1] Leitgeb, H., Untersuchungen über die Lebermoose, Heft 1, 1874, p. 64, Taf. 4.

[1] Schiffner, V., Ueber einige Hepaticae aus Japan. Oesterr. botan. Zeitschrift, 1899, nr. 11; p. 7 of reprint.

two opposite marginal notches, whilst the others are spherical and much smaller. Each gemma is borne on a slender unicellular stalk, and between them there grows out numerous mucilage-hairs. The spherical gemmae differ further from the lenticular ones in the fact that they usually begin to germinate and to produce young plants before being set free. This gemination in situ is sometimes observed in the case of *Blasia*, the gemmae of which may put out rhizoids before leaving the receptacle. It is interesting to note that the archegonia in *Cavicularia* are produced in receptacles exactly similar to those containing gemmae.

III. *Jungermanniales.* B. *Jungermanniaceae Acrogynae.* In this group, which includes the vast majority of the species of Hepaticae, asexual reproduction takes place by means of caducous shoots (normal or adventive in origin) and gemmae, these two main types being connected by transitional organs.

Caducous branches. By the dying away of the older parts of the shoot, the branches become separated and grow independently. This simple process of multiplication is of extremely common, perhaps universal, occurrence in the Acrogynae. The branches thus separated may either be those formed in the ordinary manner at the apical growing-point or adventive branches of relatively late origin. The adventive branches appear invariably to arise from the ventral surface of the stem, and in species provided with ventral scales (amphigastria) each of these branches usually appears in the axil of a ventral leaf. In most cases, these ventral branches are at least partially derived from the inner cells of the stem. The growing-point of the branch is laid down immediately behind that of the stem itself, but instead of at once growing out, as the ordinary lateral branches do, it remains dormant for a considerable time. The apical cell of the ventral branch becomes covered by a superficial layer of cells, forming a sheath through which the resting-branch breaks when the apical cell resumes its growth. In some genera, *e.g.*, *Lophocolea*, *Cephalozia*, *Kantia*, nearly all the branches are of this intercalary type and spring from the ventral surface of the stem, normal lateral branches being very seldom formed. The slender small leaved shoots ("flagella") of *Bazzania* may be cited as further examples of the same type of branching.

In cases where the growth of the main stem is arrested by the formation of archegonia, it is very common to find one or more branches arising immediately below the involucre or perianth. These "innovation-shoots," like the intercalary ventral branches,

often become detached and form new plants. In *Jungermannia* (*Aplozia*) *caespiticia*, Ekstrand[1] found within the perianth a number of young shoots, as many as fifteen in one case, arising amongst the archegonia. A still more interesting observation is recorded by Schiffner,[2] who found in *Bazzania pectinata*, collected in Amboina, a perianth from which there projected a slender shoot bearing small leaves. This shoot had arisen within the calyptra or fertilised archegonium, and appeared to spring from the base of the sporogonium itself. The latter was well developed, but had not grown beyond the calyptra, which had been ruptured by the adventive shoot. Schiffner was unable to determine exactly whether this shoot had arisen from the inner surface of the calyptra or from the base of the sporogonium itself, but the former would appear to be the more likely place of origin.

Under the heading of caducous branches may be placed the leafy "propagula" described by Evans[3] as occurring in some species of *Leptolejeunea* and *Drepanolejeunea*, which live epiphytically on trees in tropical America. Each of these "propagula" arises immediately behind an ordinary lateral leaf and may be regarded as a short bud-like branch, bearing discoid leaf-like organs the cells of which secrete mucilage; by means of these adhesive organs, the branch after separation from the main shoot becomes attached to the substratum and grows to form a new plant.

In *Frullania fragilifolia*, the hood-shaped lower lobe ("lobule" or "auricle") of each leaf is joined to the upper lobe only by a very narrow stalk, consisting of two cells, so that it readily becomes detached. Berggren[4] observed that when the lobule becomes free, or even whilst it is still attached to the plant, it gives rise to a leafy shoot. A single cell on the margin of the cup-like lobule grows and divides by intersecting walls, which cut out a tetrahedral apical cell from which the young shoot takes its growth.

In *Pteropsiella frondiformis*, a remarkable form discovered by

[1] Ekstrand, E. V., Anteckningar öfver Skandinaviska lefvermossor. Botaniska Notiser af Nordstedt, 1880.

[2] Schiffner, V., Ueber exotische Hepaticae. Nova Acta d. K. Leop.-Car. Akad., Band 60, 1893, Nr, 2; p. 260, Taf. 11, Fig. 11.

[3] Evans, A. W., Hepaticae of Puerto Rico. I. The species of *Leptolejeunea*. Bulletin of the Torrey Botanical Club, Vol. 29, 1902, p. 496. II. *Drepanolejeunea*. Ibid., Vol. 30, 1903, p. 19.

[4] Berggren, S., Jakttagelser öfver mossornas könlosa fortplantning genom grodknoppar och med dem analoga Bildningar. Akademisk Afhandling, Lund, 1865, p. 26; Tab. iv., Fig. 26-28

Spruce in Brazil, the vegetative portion of the plant consists of a branching thallus, closely resembling in appearance that of *Metzgeria* (Fig. 5). On either side of the cylindrical midrib there is a broad lamina consisting of a single layer of cells. Apical branching seldom or never occurs, but numerous branches arise ventrally from the sides of the midrib, and as each of these branches is joined to the main shoot only by a narrow base, it readily becomes detached and grows independently. The sexual organs are borne on ventral shoots which arise in the same manner as the sterile branches, but which bear well developed leaves in two lateral rows. The writer has, thanks to the kindness of Mr. M. B. Slater, F.L.S., Malton, had an opportunity of examining a large

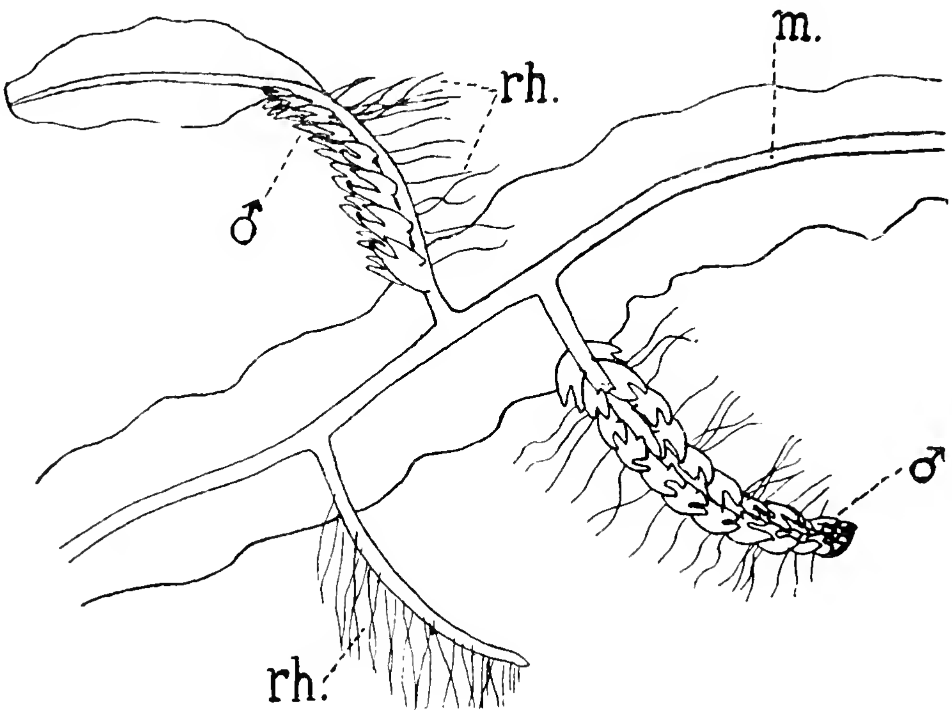

Fig. 5. *Pteropsiella frondiformis*. Part of a male plant, showing above a male branch which has, after producing antheridial bracts grown out as a thalloid shoot; below are two branches, one flagellate and rhizoid-bearing the other antheridial; *m.*, midrib; *rh*, rhizoids. × 10.

number of plants from the Spruce collection, and can confirm the observations and conclusions of Goebel on the morphology of this genus. Goebel[1] states that in the material at his disposal, the growth of the male shoots had invaribly terminated on the development of the antheridia, but the writer has found in two cases that the male shoot had resumed its growth after producing the antheridia, the apex growing out to form a flattened branch, the margins of which bore the characteristic unicellular appendages (Fig. 5).

In addition to the intercalary or adventive branches described in the preceding paragraphs, we occasionally find in the Acrogynae that adventive branches grow out from the leaf-cells or from the

[1] Goebel, K., Rudimentäre Lebermoose. Flora, 1893, Heft 2; p. 91.

superficial cells of the stem. Leitgeb[1] worked out the development of these branches in *Cephalozia bicuspidata* and in *Lophocolea bidentata*. In both of these commonly-occurring forms, the writer has found that the older parts of the plant frequently bear adventive shoots, each of which arises from a single leaf-cell or superficial stem-cell. In these old and more or less decayed parts, the cells are often filled with branched and coiled fungal hyphae and have become brown, but here and there we find cells which have retained their living protoplasm and are free from fungal attack, and it is from such cells that the adventive shoots are developed. As a general rule, the shoot springs immediately from the surface of the leaf or stem, but sometimes the parent cell grows out to form a long tube, the distal end of which swells up and undergoes repeated divisions to form the growing-point of the new shoot. As a general rule, the adventive shoot becomes detached from the parent plant at an early stage, but sometimes it remains attached until it has formed a considerable number of leaves and a few rhizoids. Such a case of vivipary was observed in *Lophocolea bidentata* by Massalongo,[2] who figures a leaf bearing three young plants; two of them replace the pointed lobes of a normal leaf and are furnished with rhizoids. As will be pointed out later in dealing with gametophytic regeneration in Hepaticae, adventive growths of this kind are often abundantly produced on leaves which have been isolated and kept under cultivation, but it is interesting to find that the process of regeneration may also occur in nature, the viviparous shoot reaching a fairly advanced stage of development before becoming severed from the parent plant.

[1] Leitgeb, H., Untersuchungen über die Lebermoose, Heft 2, 1885, p. 38.

[2] Massalongo, C., Sopra un interessante caso di viviparità nelle Epatiche. Bullettino della Soc. bot. ital., 1901; reprint of 4 pp.

(To be continued).

NOTE ON GEOTROPISM OF GRASS-HAULMS.

IN Sachs' *Arbeiten* iii., p. 509, Noll described the curious effect of fixing a grass-haulm immovably in the horizontal position. Under these conditions the lower half alone grows, demonstrating Noll's contention that the decisive feature in geotropism in increased growth on the convex, rather than inhibition on the concave side. The haulm being fixed, the growth of the lower side cannot produce curvature, and the effect, as Noll describes it, is the appearance "of peculiar outgrowths and weals (Schwielen) on the lower side, in which the strong growth-tendency of the cells expresses itself.' As this description implies, and as Noll's figures show, the growth is principally at right angles to the longitudinal axis of the pulvenus. The tendency to growth must, however, be primarily in the longitudinal direction, and the figure (for which I am indebted

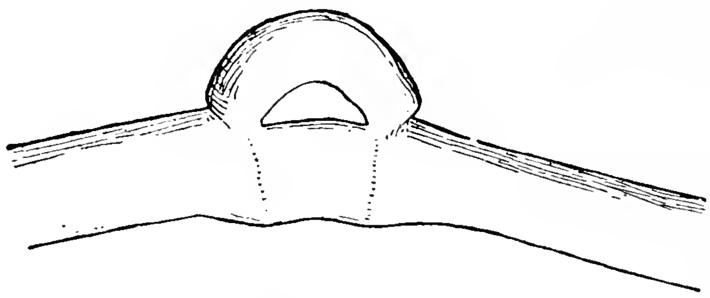

Fig. 1. × 3.

to Miss Pertz) taken from a specimen obtained in class-work at Cambridge shows, in addition to a growth in thickness, the existence of longitudinal growth which has been sufficient to cause a rupture of the pulvinus. The result may, perhaps, be due to the method employed by us, and described in Darwin and Acton, *Practical Physiology of Plants*, Edit. iii., p. 166. Noll prevented curvature by inclosing the haulms in narrow glass tubes: we fix the grass-stalks firmly into a sheet of cork, placing them at right angles to a groove cut in it; the haulms being so arranged that the pulvini are over the groove. As far as the essential feature—the prevention of curvature—is concerned, our method is the same as Noll's; but the pulvini not being in contact with a glass tube are free to produce any form of outgrowth.

Bot. Lab., Cambridge, FRANCIS DARWIN.

June 11th, 1903.

THE FLORA OF THE GALAPAGOS ISLANDS.

IN a recent number of the *Proceedings of the American Academy* (vol. xxxviii. pp. 77-269), Dr. B. L. Robinson gives an account of the flora of these islands. He has brought together all the available material and his memoir represents the extent of our knowledge of the origin and distribution of plant-life on the five larger and twelve of the smaller islands. Our knowledge of the latter is largely owed to the recent expedition of Messrs. Snodgrass and Heller. The collections include some fungi and algae which have been worked out by Professor Farlow, and among which are a new lichen and three new seaweeds, one, *Herpophyllon*, a new red seaweed of doubtful affinity. There are also a few bryophytes and 59 pteridophytes. Three out of the 55 ferns are endemic, that is about 5 per cent. The total number of seed-plants (including a few introduced species) is 531, made up of 445 species, 17 varieties, 19 forms, and 50 indeterminate; of these 202 species, 15 varieties and 19 forms are endemic, making 44·4 per cent. of the whole flowering flora. More than half (130) of these endemic plants are confined to a single island. There are only two endemic genera, both of the order Compositae, *Lecocarpus* which is monotypic, and *Scalesia* with 18 species.

As with most insular floras, the vegetation of these islands is striking rather by the absence of certain great groups than by the number and diversity of the genera and families represented. Thus among pteridophytes arborescent forms on the one hand and the filmy ferns on the other are wanting. There are no gymnosperms, and if we except the grasses and sedges which are well represented, there are very few monocotyledons. Of dicotyledons, the families best represented are Amarantaceae, Nyctagineae, Aizoaceae, Leguminosae (about 10 per cent. of the seed-plants), Euphorbiaceae (about 12 per cent.), Malvaceae, Cactaceae, Convolvulaceae, Boraginaceae, Verbenaceae, Labiatae, Solanaceae, Rubiaceae, and Compositae (about 13·5 per cent.) Several great families, widely distributed and abundant in the tropics of continental America, such as Sapindaceae, Myrtaceae, Melastomaceae, Lythraceae, and Onagraceae, are scarcely or not at all represented in the flora of the archipelago. Altogether 72 families of vascular plants, including 232 genera, are known from these islands, 39 of the families include endemic forms.

The orders richest in endemic species are Compositae with 39, Amarantaceae with 29, Euphorbiaceae with 25, Rubiaceae with 16, Gramineae with 13, and Boraginaceae with 12, Leguminosae; Cactaceae and Convolvulaceae contain 6 to 8, and 29 other orders contain 1 to 5 endemic species.

The lower slopes of all the islands are relatively sterile, arid and rough, much of the surface being covered with lava-blocks. The air although not excessively hot is very dry, and the predominating perennial vegtation is of a small-leaved xerophytic type, composed of scattered shrubs and undershrubs, or wiry herbs and grasses, above which rise arborescent species of *Cactus and Opuntia.* On the higher islands which rise into moister air.strata, a much more luxuriant mesophyte vegetation prevails. Trees, if we except the arborescent cacti, occur chiefly upon the upper parts of the islands

and never attain great size. Many of the trees and shrubs are armed with spines or thorns, *e.g.*, *Mimosa*, *Acacia*, *Parkinsonia*, *Cereus*, *Opuntia*, and *Zanthoxylum*. Climbers are neither so numerous or conspicuous as in the tropical parts of the American continent, moreover they are herbaceous, the woody liàne so common in tropical jungles, being almost unknown upon the islands. The chief climbing genera are *Boussingaultia*, *Cissampelos*, *Rhyncosia*, *Cardiospermum*, *Ipomoea*, and three cucurbits, *Elaterium*, *Momordica* and *Sicyos*.

Epiphytes, which occur only at the higher altitudes, are neither abundant nor showy; the chief are a *Tillandsia*, an *Epidendrum* and several *Peperomieae*. Of phanerogamic parasites there are four species of *Phoradendron* and two of *Cuscuta*. Flowers are generally small and inconspicuous, and in most cases regular and simple in structure.

As regards its affinity the flora is an outlying portion of the American flora, with a strong specific differentiation, but it is impossible to trace its relationship closely to any one section of the Pacific American vegetation. Nearly all the plants are identical with or obviously related to, species of the Sierras and Andes or of the Pacific slope between Lower California and Northern Chili. The xerophytic elements show a considerable resemblance to the desert flora of Southern Peru and the drier parts of the Andes, while the mesophytes correspond most nearly to plants of Ecuador, Colombia, Central America and Southern Mexico.

Two views have been advanced regarding the origin of the islands. According to one view they are pelagic islands built up from the sea-floor by volcanic action; according to the other they are continental islands, tops of mountains formerly a part of the mainland, and now separated from it by subsidence. The first view is supported by the following facts:—(1) All parts of the islands now visible are obviously of volcanic origin. (2) The islands are separated from the mainland by a very considerable depth of ocean (more than 1,500 fathoms.) (3) The western coast of South America shows no signs of subsidence, but rather of marked elevation in geologic time. In accordance with this theory, the flora is assumed to have been brought by wind, oceanic currents and migratory birds. The islands lie in the course of fairly constant trade-winds, and the great ocean-current which sweeps along the west coast of Mexico, and the Humboldt current which runs northward along the coast of Chili and Peru, both turn westward just in the equatorial belt where the islands lie. Alexander Agassiz states that the velocity of the currents in the Panama district is very great, so that seeds, fruits, and masses of vegetation harboring small reptiles or even large ones, as well as other terrestrial animals need not be long afloat before they might be safely landed on the shores of the Galapagos; and as Hooker has shown, a large proportion of the plants are provided with special means of seed-dispersal.

Against this view of the pelagic origin of the flora, Dr. Baur has adduced what he terms the harmonic character of the flora and fauna of the islands. Many plants and animals on the different islands are nearly related to each other without being exactly the same. For instance each of several islands has a peculiar species of *Scalesia*, one of the two endemic genera. There are also several different forms of *Euphorbia viminea*, several very nearly related

species of *Acalypha*, &c. In many instances these forms are confined to a single island, and in the majority of cases each form is more closely related to those of the other islands than to any continental ally. On the theory of origin by subsidence, these harmonic relations are readily explained. If the islands were once united and then separated by subsidence, the remnants of their common flora and fauna, persisting upon the different islands, would have diverged not only from the continental types but from each other. From the depth of ocean between the archipelago and the mainland it would naturally be inferred that the islands were cut off from the continent before they were divided from each other, and this will explain the greater difference between the forms and the continental type than between the forms themselves.

Dr. Robinson, however, suggests an explanation which will accord with the theory of emergence.

If we assume (1) that seed-transference between the mainland and the islands or between the islands themselves, does not occur in the case of particular plants oftener, on the average, than once in several years, and (2) that plants have multiplied on the islands as rapidly as they have frequently been observed to multiply elsewhere, it becomes as easy to account for the existence of a harmonic flora on islands of emergence as on islands of subsidence.

On these premises an insular form having started its divergence from the continental type, would be likely to become more and more differentiated, and, owing to its existence in large numbers, would not be much affected by the occasional arrival of isolated and scattered seeds from the continent. Similarly if seeds of the new form were carried to other islands of the archipelago, further specialized races might arise bearing much the same relation to the original insular form as that did to its continental progenitor; and these secondary forms would be similarly as little affected by subsequent rare and isolated seed-arivals. Thus unchecked, the races might develop into more and more highly differentiated forms and varieties, and ultimately into well-marked species characteristic of particular islands.

That this assumed infrequency of successful seed-transference does obtain in the case of the Galapagos, is clearly shown by the existing diversity in the floras of the different islands—a condition which could not continue if seed-transference were very common. The infrequency may be explained by the arid and sterile shores, which offer to most seeds washed ashore by oceanic currents a very poor chance of successful germination.

Finally, Dr. Robinson draws special attention to the relation which the proximity of the different islands bears to likeness in their florulae. Although the islands are very different in altitude, climate and fertility, the diversity in their vegetation is greater than we should expect. The common element between any two rarely exceeds 75 per cent. and is often less than 50 per cent. Moreover these differences stand for the most part in no relation to the distance of the islands from each other, or to the depths of the intervening channels. The florulae of Albemarle and Charles, islands at opposite ends of the archipelago, are more alike than either is to that of intervening islands, and cases in which proximity between two islands is associated with marked floral similarity are quite the exception. Such anomalies must find their explanation in peculiarities of

climate and soil, together with an element of chance, arising partly from imperfect exploration and partly from the accidents of seed-dispersal.

But although these relation are not fully explained by the theory that these are islands of emergence casually seeded, they are much less in accord with the theory of subsidence. For if the florulae were remnants of a common flora persisting upon islands separated by gradual subsidence, it is evident that those islands would possess the most floral similarity which were nearest together and divided by the shallowest channels, since these would have been separated from each other more recently than the remoter islands, which are cut off by a greater depth of ocean. Hence the botanical evidence, so far as it has yet been made out, is opposed rather than favorable to the subsidence theory. A. B. RENDLE.

TWO RECENT NATURE-STUDY BOOKS.

FIRST STUDIES OF PLANT LIFE, by George Francis Atkinson, Ph. B., Professor of Botany in Cornell University. Boston, U.S.A., Ginn and Company (British Headquarters, 9, St.Martin's Street, W.C.) 1902.

NATURE STUDIES (PLANT LIFE), by G. F. Scott Elliott, M.A., Cantab, etc., Lecturer on Botany, Glasgow and West of Scotland Technical College etc. London, Blackie and Son, 1903.

IT must always be a more difficult matter to write a successful book intended to appeal to children, than a good treatise for adult students. Not only must the author have that thorough knowledge of his subject, and those gifts of logical arrangement and clear exposition, which are essential to the production of a sound work of any sort, but he must have the powers of sympathy and imagination which enable him to put himself in the place of the fresh young mind, whose method of attacking the problems around him are often so different from those of the grown and "educated" one. At the same time, he must above all things avoid the appearance of "writing down" to his audience, for nothing irritates an intelligent child more than that. In short, the combination of qualities needed is necessarily a rare one, and there are very few really first-rate children's books of science.

Professor Atkinson's attempt is certainly strikingly good. He presents the leading facts of the life and work of plants in absolutely the right spirit, and in a vigorous and attractive style. At every point that can possibly be illustrated by direct observation or simple experiment the reader is told how and where to make the observation or how to perform the experiment; and the 261 pages of large type are illustrated by no less than 308, for the most part excellent, cuts and photographs, representing the most varied things, from the bursting into flame of a glowing splinter in the oxygen given off by the leaves of a water-plant in sunlight, to American desert-communities and the "Struggles of a White Pine." The great advantage the author gains from being a thoroughly trained professional botanist is at once obvious here, besides accuracy of statement (not always a conspicuous feature of this class of work), a general breadth of treatment and a correct perspective are obtained; while many of the experiments, simple as they are, would only have suggested themselves to one well acquainted with

modern practical plant-physiology, and the concluding section on the "Battles of Plants in the World" gains everything from the modern study of ecology, so widely developed in America during the past few years.

The faults of the book seem very trifling. We are not sure that putting a number of the sentences in the form of questions, evidently intended to keep the mind of the reader active, is a good plan. It breaks up the exposition, and tends to turn the "crispness' of the style into "choppiness." Furthermore, while some of the questions are answered in the context, others are not, but are supposed to be left to the observation of the reader, and this has rather a bewildering effect, A few statements are a little misleading or obscure. On page 119, for instance, it is implied that the formation of starch always precedes that of living substance in the plant, which is hardly accurate; while on page 193 it is stated that "there is a royal bit of life substance in the very young embryo case, known as the germ or egg." The use of the adjective "royal" here, without explanation or comment surely is a little strange. Occasionally the author's outbursts are rather amusing. After telling the "life stories" of Ferns, Mosses and Mushrooms, he says: "Some will tell you that such interesting plants as the ferns, mosses and puff-balls are *cryptogams*, and that therefore you should not try to read the stories they have to tell. But why call them cryptogams? That is a terrible word that ought to be blotted out of the English language. Why not call them plants, as they are? They are just as much God's creatures as the dandelion and thistle and smart-weed. They are just as interesting, too, and mean as much in our lives as they do." We wonder what the average child will make of this. Or is it intended as a mild rebuke to a possible ignorant and pedantic teacher? Some of the half-tone reproductions of photographs of vegetations are not so good as they might be, though others are excellent.

But we must congratulate Professor Atkinson very heartily on the work, which ought to be of considerable use on this side of the Atlantic, the only drawback being the fact that many of the native American plants mentioned are not found in England.

Mr. Scott Elliot's book has a different object. It "has been written" says the author "with the view of helping those non-professional lovers of Nature Study" who are really interested in the mystery of Plant-life Mr. Scott Elliot is very anxious "as far as possible, to do without technical terms." "In England," he says in his preface, "the terminology of Botany is fast becoming a sort of Chinese alphabet, which will require so much time to master, that nothing of a life-time will be left in which to use it in the study of Nature." This rather suggests that a student learns all the botanical terms in current use before he begins to use any of them! The student who tries this plan is certainly to be commiserated. The more usual method, we should have thought, is to learn such terms as are necessary in order to have exact names for things he wants to read about or allude to. No one will ever acquire exact knowledge of any branch of the science unless he does so much, and no serious botanist we have ever met desired more terms than were "necessary" in this sense. Of course, in "popular classes," that

is in classes the students of which have had little or no training in the exact methods and the exact language of science, (and in popular books too), it is most important to "go slowly," to introduce descriptions of things and processes and the ideas connected with them (and consequently the names used for the things and processes) one by one, with the most abundant illustration and "cross-reference"; but to imagine that it is possible to "do without technical terms in the study of plants is surely a delusion. As a matter of fact the author of the work under review scarcely makes the attempt, when it comes to the point, and in some instances really goes further than is at all needful. In chapter viii. on "The Stem," for example, he describes its microscopic anatomy and uses quite a number of terms. We cannot think the description or the terms are necessary in the general scheme of the book, and as it stands the first part of the chapter can hardly make any other than a confused impression on the reader's mind. In other places, again, technical terms are introduced rather gratuitously. For instance, on page 179 we are told that *Volvox* "reminds one of the *blastosphere* of the animal world," without a word of explanation as to what a "blastosphere" may be.

The book as a whole errs, we should say, in being too crowded with miscellaneous information—the student is hardly given time, so to speak, to get firm hold of a fact or idea before he is hurried on to something else. At the same time it contains a great deal of much interest, and the general notion of making the reader think about plants as living things, with the most complicated life-struggles and processes always going on in connexion with them is well and consistently adhered to. The best part of the book, in our opinion, is the concluding chapters on the "History of the British Flora," "Woods and Forests" and "The Influence of Man." These contain accounts, for the most part capital as well as novel, of British vegetation and the effect of human agency upon it, treated from a historico-biological point of view. A word of caution would have been desirable in introducing the consideration of Woods as *Organisms*. Though the consideration of "plant-associations" as more or less integrated "individuals" is of the greatest value, it should not be forgotten, as it sometimes tends to be by the more enthusiastic of the followers of Warming and Schimper, that such an "association" really possesses far less integration than a human "society," which in its turn falls far behind that of an individual organism.

THE STELAR THEORY.[1]

IN the form of a thesis for the degree of doctor in the University of Groningen, J. C. Schoute has afforded us a really important contribution to the above subject. It is, to our mind, an exceptionally clear and thorough summary of the facts and theories bearing on every branch of the great problem, yet is at the same time supported by very careful and pointed original observations, and, what is of chief importance, rounded off by that comprehensive grasp of, and

[1] "Die Stelär-Theorie"; Groningen, 1902.

genuine insight into, the problems dealt with, which is sufficiently uncommon in our days. In fact, the author exhibits the powers not only of a careful observer of detail, but also of a capable generalizer on the broader issues at stake.

The book is divided into two parts of which the first deals with "The Stelar Thery and the History of Development [Ontogeny]" and the second with "The Stelar Theory and Comdarative Anatomy."

The first chapter is entitled "*Facts connected with the differentiation of tissue into dermatogen, periblem and plerome*," and contains a critical discussion of the literature on the subject. The author concludes that Hanstein's primary divisions of the tissue are inconstant, and often obscure, irregular or almost absent in the embryo of Phanerogams, and altogether wanting in that of the Vascular Cryptogams; they are equally absent in the apical meristem of the latter group. As regards the Phanerogams, although in some cases the apical differentiation of the stem is clear and sharp, yet in other cases this is by no means the case; so that, consequently, much importance cannot be attached to the Hanstein division. It is, however, more constant in the root. The tissues of *lateral* organs do not arise from the corresponding tissues of the organs bearing them. Chapter 2 is headed: "The Correspondence between the Primary Tissues of Hanstein and these of Van Tiegham," and its object is to determine whether the dermatogen, periblemand plerome of the apical region give rise respectively to the epidermis, cortex and central cylinder of the lower (mature) part of the stem. The following are his conclusions, founded on original observations. In those *roots* where, at the apex, there exists a sharp division between periblem and plerome, the cortex arises from the former and the central cylinder from the latter. In *stems*, on the contrary, and in the only case in which the apical divisions were regular, *viz.*, in *Hippuris*, this correspondence fails to obtain, for in this plant the endodermis ("Schutzscheide") arises, along with a few cortical layers, from the plerome. In those *roots* in which the cell-divisions do not take place so regularly, there is found, as in the great majority of stems, absolutely no correspondence between the apical differentiation and Van Tieghem's division. In view, therefore, of the fact that the Hanstein division of the tissues holds good only for a few roots and for one single stem, the idea that that division can be of any phylogenetic and morphological importance must be rejected. Even the dermatogen does not always correspond to the epidermis, though it much more frequently gives rise to the latter than do periblem and plerome to the cortex and central cylinder respectively. As inaugurating the second part of the book, chapter 3 treats of "The Limit between Cortex and Central Cylinder in Stems" of the three great classes of Phanerogams. In Gymnosperms no definite endodermis exists, but nevertheless a sharp actual distinction obtains between cortex and central cylinder. In Monocotyledons a monostelic structure with clearly-differentiated endodermis is very frequent. In some stems, however, a limit between the two main tissues cannot be made out; in others this limit is obvious, but a specialised sheath does not exist. Yet, as *all* Monocotyledonous stems agree in their general structure, the main divisions of Van Tieghem will apply, in spite of certain variations, to all cases. As regards Dicotyledons the distinction between

cortex and cylinder is much more generally pronounced than in the last class; the author cites seven plants only in which the limit by means of an endodermis is obscure. Owing to the agreement in general structure between the stems of Gymnosperms and Dicotyledons it follows that cortex and central cylinder are respectively homologous parts in each. The same must also hold good for Monocotyledons, for Von Mohl has shewn, from a study of stelar development in Palms, that the scattered arrangement in these is founded on the same basal plan as the hollow cylinder of Dicotyledons.

Under this section of the book is brought the "Comparative Anatomy of the Young Plant" (of which chapter 4 treats), for the reason that the author considers "development" or "ontogeny" as being concerned with the differentiation of the various tissues from the meristem; and that in studying the development of the young plant we are concerned with that branch of comparative anatomy which compares together, not different plants, but the different parts of one and the same plant. It is a special division of the subject concerned with the study of *fully-formed*, yet early-developed organs. The various English and American authors who are identified with this method of investigation are noted and Van Tieghem's theories shortly discussed, the conclusion arrived at with regard to this latter author being that, although in some points, especially with regard to the subjects of polystely and astely, a revision of his views is desirable, yet the results of the researches of the various authors mentioned constitute an excellent confirmation of his main position that the *monostelic* is the primary structure in all vascular plants.

Finally, in the last chapter "General Considerations and Conclusions," the wide sweep of vision and enlightened ideas of the author shine forth. We are here again forcibly reminded, and at greater length, of the comparative worthlessness of developmental data in determining the morphology of the various tissues, and are rather directed to the *comparative method* as the only reliable agency for this end; both Van Tieghem and Strasburger being quoted in support of this position. Interjected in the midst of the chapter, in a footnote, appears a glossary of all the terms adopted by the various authors in connection with the stelar theory. Considerable attention is devoted to the position assumed by Jeffrey, in opposition to Van Tieghem, that the pith belongs, not to the stele, but rather to the cortex, as shewn by the presence of an "inner endodermis," the *continuity* of pith and cortex through the leaf-gaps, and the absence of a pith in many stems of seedling plants. The same idea is held by Faull and by Farmer and Hill. It is with able lance that our author enters the lists of discussion on the burning questions connected with stelar morphology. In the first place he considers that Jeffrey, in common also with Van Tieghem, Strasburger, and Gwynne-Vaughan, labours under a fundamental fallacy in regarding the ontogenetic continuity of any two tissues as affording the criterion of their homology. One author only, *viz.*, Boodle (whom he quotes) has had the insight to see otherwise. No! "if cortex and pith," says our author, "were homologous, this would mean that the tissue which, in the ancestors of the plants concerned, constituted the cortex, reappears in their modern representatives partly as cortex and partly as pith. The cortex must, therefore, in the course of the phylogenetic development have become intruded

into the central cylinder." In no other sense than this can *homology* possess any meaning whatsoever. But to this origin of the pith our author will not subscribe. "Doubtless," he continues, "the pith has arisen phylogenetically from stelar cells—at least if the solid vascular strand constitutes the phylogenetically oldest stage—; there can therefore in that process be no more question of intrusion than there exists at present in the case of the seedling-plant." This is supported by the detailed facts of development of the pith described by Farmer and Hill in *Angiopteris*.

Then with regard to the question as to the value to be attached to the presence of the endodermis in the form of either a protective or a starch-bearing sheath, our author holds that Jeffrey, Van Tieghem, and others have greatly exaggerated this. The endodermis may, from its well-known histological characters, be generally recognised as the morphologically inner layer of the cortex; these characters are therefore of importance for the determination of morphological relationships. But it by no means follows from this that every layer which is histologically differentiated as a "protective sheath" is necessarily an endodermis in this sense. The idea of Farmer and Hill that there is "a strained and artifical criterion as to the boundary of the stele" has arisen solely from the fact that the "protective sheath" ("Schutzscheide") which is a histological diffentiation, has been confused with the morphological conception of the endodermis.

Erroneous views have also been put forward by Pitard, with regard to the morphological value of the *pericycle*. The author observed this layer in the older plant–organs becoming torn, and cells of other tissues intruded between the pericycle cells; but the conclusion he arrives at—that when in this way the activity of the tissue ceases, it is no longer to be regarded as a pericycle, is as absurd and erroneous as it would be to conclude from the fact that epidermis and cortex are often cut away by an internal periderm and are thus actually absent, that these tissues possess no morphological value as such.

Our author next discusses and disposes of the views of Van Tieghem with regard to "Polystely" and "Astely" as applied to the stem, showing that these are merely modifications of the fundamental monostelic condition. But in *leaves* it is different; although in many of these monostely is clearly present in the petiole, yet from the fact that in the lamina the bundles always exhibit an independent course and a distinct sheath, and the absence of any data to show the derivation of the leaves of modern plants from monostelic leaves, it appears best to conclude that the structure of the lamina has always been different from that of the stems and petioles with their rounded contour. True *astely* as contrasted with monostely, exists therefore in the leaf-lamina; while Strasburger's term "schizostely" may be applied to that variety of monostely occurring in the stem in which a "protective sheath" is present around each bundle. Yet the author admits that astely may possibly be a modification of monostely, and if so must be of greater importance than schizostely because more widely distributed and more distinctively modified; he admits the presence in some plants of a schizostelic structure in the petiole or large veins forming a transition from the monostelic condition of the stem

to the astelic conditions of the lamina; and he admits also that the limits between astely, schizostely and monostely can be only arbitrarily defined.

This conception of the leaf the reviewer feels altogether unable to agree with; in his opinion the leaf must possess throughout the same fundamental structure as the stem; space, however, will not permit of his enlarging upon this idea.

The author's conclusion with regard to Van Tieghem's stelar theory is that in its essential features it may be retained unaltered, seeing that monostely is present in stems and roots, and astely in leaves, in practically the great majority of cases.

In the opinion of the reviewer the book is the best general treatise on the stelar theory which has yet appeared.

W.C.W.

THE LONDON BOTANICAL SOCIETY.

The June Meeting of this Society was held at the Royal College of Science on Tuesday, June 16th, Dr. D. H. Scott in the chair.

Miss Lorrain Smith exhibited and gave a short account of some interesting microscopic Fungi new to Britain. One of these had been found only once previously, in Silesia, before it turned up recently in the New Forest. The opinion was expressed in the discussion that such apparent anomalies of distribution were the result of ignorance, several analogous cases being cited.

Miss Ethel Sargant communicated some preliminary observations made by herself and Miss Agnes Robertson on the vascular tissue of the scutellum of the Maize, calling attention to some apparently undescribed and most interesting points in the structure of this organ.

Dr. F. E. Fritsch exhibited three slides of Thames phytoplankton, illustrating the differences between the plankton of a backwater and that of the main stream.

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THE PHENOMENON OF "DOUBLE FERTILISATION" IN ANGIOSPERMS.

AN HISTORICAL SKETCH.

OF all botanical studies none is more important or fascinating than those concerned with the process of fertilisation in the higher plant and with the events following this within the embryo-sac of the devoloping seed. It is to tireless and ingenious investigators like Professor Strasburger of Germany that we owe the accumulation of facts with regard to the various phenomena which precede the development of the embryo and the endosperm within the ovule.

Yet, notwithstanding all this industry and refinement of method in research, one of the most important and remarkable links in the complicated processes connected with fertilisation and endosperm-formation had been, until quite recently, even by men like Strasburger, entirely overlooked. I refer to what is now commonly known as the phenomenon of "double fertilisation," the discovery of which did not occur until some five years ago, *viz.*, by two botanists quite independently the one of the other: Nawaschin[1] in Russia, and Guignard[2] in France. Priority of publication, however, fell to the lot of the former.

The cell which eventually grows into the embryo-sac is the homologue of the megaspore of the heterosporous Pteridophytes, and is, in most cases, one of the products of division into three or four cells of the primary mother-cell in the nucellus. Absorbing, as a rule, its sister-cells the incipient embryo-sac developes apace and its nucleus

1 "Resultate einer Revision der Befruchtungsvorgänge bei Lilium Martagon und Fritillaria tenella." (Bulletin de l' Acad. Impériale des Sciences, de St. Petersbourg; Vol. ix., 1898, No. 4).

2 "Sur les anthérozoides et la double copulation sexuelle chez les végétaux angiospermes." (Comptes Rendus, 4 April, 1899; Revue générale de botanique, Vol. xi, 1899; Volume jubilaire de la Société de Biologie, Paris, 1899).

comes to occupy a central position in the cell-cavity. At maturity of the cell this *primary nucleus* divides into two daughter-nuclei, each of which travels to one end of the sac. Then each divides by two successive divisions until four nuclei are formed at each end of the sac. One of these four from each end then travels to the centre of the sac, and, sometimes before, sometimes after, fertilisation takes place, these two *polar nuclei* fuse together to form the *definitive* or *secondary nucleus* of the embryo-sac. Meanwhile, each of the three nuclei at the micropylar end of the sac becomes invested with protoplasm enclosed by a delicate membrane; a pair of these cells, usually somewhat elongated, at the extreme end of the sac become the *synergidae*, while the third and larger cell becomes the *oosphere* or egg-cell. At the chalazal end of the sac three antipodal cells are formed, and these are often much more conspicuous than the cells at the micropylar end.

Hofmeister[1] considered that all the nuclei of the sac possessed primitively the same value and any one of them could develope into an embryo. The sole function of the antipodals was that of elaborating substances for the embryo.

Vesque[2] and Warming[3] both regarded the embryo-sac as the product of fusion of two cells, and the four nuclei finally formed at each end of the sac were the representatives of the spores resulting from the divisions of these two spore-mother-cells.

Guignard[4] held that all the cells in the sac were endosperm-cells; that the oosphere was a reduced archegonium; that the synergidae were endosperm-cells which had become adapted to a new function; and that the antipodals are either an organic residuum of the sac or a reduced prothallus; but he eventually regarded the prothallus as consisting of the sexual apparatus, antipodals and the two polar-nuclei.

Hartog[5] believed that, as a result of two successive divisions of

[1] "Neue Beiträge zur Kenntniss der Embryobildung der Phanerogamen"; (Abhandl. d. Königl. Gesellsch. d. Wiss.; Vol. v., p. 671).

[2] "Développement du sac embryonnaire des Phanérogames Angiospermes"; Ann. d. Sciences Nat. Bot., ser. 6, Vol. vi., 1878.

"Nouvelles recherches sur le développement du sac embryonnaire"; Dittó, ser. 6., Vol. viii., 1879.

[3] "Bemerkungen über das Eichen"; Bot. Zeit. 1874.
De l' Ovule"; Ann. d. Sci. Nat. Bot. ser. 6, Vol. v., 1878.
Bull. de la Soc. Bot. de France, Vol. xxviii., 1881.
Ann. d. Sci. Nat. Bot. ser. 6, Vol. xii., 1881.
Ann. d. Sci. Nat. Bot. ser. 6, Vol. xiii., 1882.

[5] "Some Problems of Reproduction: a Comparative Study of Gametogeny and Protoplasmic Senescence and Rejuvenescence." (Quart. Journal Microx. Science, Vol. xi., 1891).

the primary nucleus of the sac: "four prothallial cells are formed; of these two in the mean position [the mother-cells of the oosphere and upper polar-nucleus and of the uppermost antipodal and lower polar-nucleus respectively] are gametogonia, which by a mitotic division form four gametes, three functional, one arrested. The apical cell [of the original four] forms an archegonium reduced to a two-cellular neck [synergidae]; the basal cell forms two cells constituting a barren archegonium or mere prothallial cells" [the two lower antipodals]. The definitive or endosperm-nucleus he regards as a zygote formed by fusion of two gametes: the two polar nuclei.

Nawaschin in 1898 published the following epoch-making observations: that whenever a pollen-tube was seen in contact with the embryo-sac *both* male nuclei were observed in the latter, were seen to have an almost cylindric long-club-shaped appearance, and to exhibit a worm-like contortion; they lay free in the sac and so close together as to appear like a single body. One of these two nuclei travelled to the ovum, the other to the upper polar-nucleus, to which latter it became applied; both nuclei retained their worm-like character. During the time that the one male nucleus was becoming more and more closely applied to the ovum, the polar-nucleus, along with the second male nucleus with which it was in contact, travelled to the other polar-nucleus and became attached to the latter in the middle of the sac. All the nuclei remained separate and distinct until the prophases of their division. The second male nucleus, which by this time had lost its worm-like shape, was smaller, richer in chromatin, and possessed a coarser chromatin net-work than the polar nuclei, the lower of which latter is considerably larger than the upper. The character of the separate nuclei and composition of the nuclear groups were observed in a great number of fertilised ovules, so that there can be no doubt of the phenomenon being a constant one. Fusion of the three nuclei took place only after the prophases of division were completed; the same being true with regard to the fusion of the other male nucleus with that of the ovum. The formation both of the embryo and the endosperm was normal; in *Fritillaria tenella* the embryo, after reaching one-third of its size, died away, and the endosperm became absorbed. The ripe seed of *Lilium Martagon* contained a normal embryo. Nawaschin believed that, from the peculiar shape of the two male nuclei in these plants, they possess an independent movement like that of worms.

His theoretical conclusion with regard to these phenomena is that we have before us in these plants a species of *polyembryony*, in the form of a pair of twin-embryos exhibiting a very dissimilar and unequal development, the one remaining thallus-like, in the form of the endosperm, and becoming eventually absorbed by the other. His view is based on the fact that the normal endosperm arises as the result of the fusion of one of the male nuclei with the *sister-cell of the ovum, i.e.*, with one of the female nuclei; and that therefore we have as much right tospeak of this fusion as a *sexual act* as in the case of the actual process of fertilisation itself. At a somewhat later date Nawaschin[1] observed "double fertilisation" in certain Dicotyledons. In the case of *Helianthus* the male nuclei were seen greatly to resemble spermatozoids, the polar nuclei were observed to fuse *before* fertilisation of the ovum, and the product of this fusion—the embryo-sac-nucleus—after copulation with the second spermatozoid was seen to divide rather earlier than was the case with the fertilised oosphere. In *Rudbeckia* similar phenomena occurred. Fusion of the polar-nuclei before fertilisation of the ovum was also observed in *Delphinium elatum*. It is an interesting fact that Merrel found elongated, spirally-twisted bodies (=spermatozoids) in the pollen grain of the Composite, *Silphium*.

Guignard essentially confirms Nawaschin's observations. He states as a result of his own labours on *Lilium Martagon* that union of both polar nuclei may precede their fusion with the vermiform sperm-nucleus and that the latter may subsequently become applied to *both* polar nuclei, but in some cases the sperm-nucleus was observed to fuse primarily with the antipodal polar-nucleus; more frequently however, copulation with the egg-polar-nucleus is the first process, because the latter is the first of the two met with by the sperm-nucleus as it passes down the sac. Guignard regards, in contradistinction to Nawaschin's view, the union or fusion of the sperm-nucleus with the polar nuclei as a case of *pseudo-fertilisation*, on the following grounds. In *true* fertilisation both sexual nuclei have the same reduced number of chromosomes, whilst the lower polar nucleus, as at any rate is known to be the case in *Lilium*, contributes a larger number of chromosomes to the fusion, with the result that the product of copulation of sperm and polar-nuclei possesses a greater number of chromosomes than does the fertilised ovum.

[1] "Ueber die Befruchtungsvorgänge bei einigen Dicotyledoneun" (Berichte der deutsch. Bot.Gesellschaft, vol. 18, 1900).

Some further observations by Guignard[1] on *Tulipa Celsiana* and *T. sylvestris* revealed the fact that the various nuclei of the embryo-sac in these two plants were very irregularly arranged and more or less similar in appearance. The lower polar nucleus, which is morphologically different from the upper one, being often larger and with denser granulations, is situated at the base of the sac, below the antipodal nuclei. The antherozoids are elongated, but not spirally twisted, and are both equivalent. The oosphere is first fertilised. The second sperm-nucleus was seen fusing with the upper of the two polar-nuclei, hence union between these latter is a late occurrence in these plants. The second sperm-nucleus and the two polar nuclei fuse together as three distinct individualities, which gradually become less and less marked and finally vanish. He observed that at the moment of division of the fertilised ovum the sac contained four endosperm-nuclei. The phenomena above described hold good for the two species mentioned; but the different races of cultivated Tulips, on the contrary, agree in this respect with the Lily and *Fritillaria*.

This author further observed[2] "double fertilisation" in several other orders of plants, such as Compositae, of which five or six genera were investigated, with the result that his obervations largely coincided with those of Nawaschin on *Rudbeckia*. In Ranunculaceae[3] the genera *Caltha*, *Ranunculus*, *Helleborus*, *Anemone*, *Clematis* and *Nigella* were examined. The two male-nuclei in these plants are spindle-shaped while within the pollen-tube, becoming elongated as they pass into the sac; they rapidly fuse with the two nuclei of the sac. In *Nigella damascena* the larger size of the male nucleus which fuses with secondary nucleus of the sac is correlated with the fact that the latter divides *before* the fertilised ovum. At the time of endosperm-formation the fusion of the male and female nuclei in the oosphere is not completed, and even after fifty endosperm-nuclei are formed in the sac the ovum remains still undivided. The same phenomenon was observed in *Anemone nemorosa*. Quite recently[4] the order Cruciferae revealed the same

1 "L'appareil sexual and la double fécondation dans les tulipes" (Annales des sciences naturelles, ser. 8, vol. xi., 1900.

2 "Nouvelles recherches sur la double fécondation chez les végétaux angiospermes" (Comptes Rendus de l'Acad, des Sciences, vol. 131, 1900).

3 "La double fécondation chez les Renonculacées" (Journal de Botanique, Dec. 1901).

4 "La double fécondation chez les Crucifères" (Journal de Botanique, Nov. 1902).

phenomenon of "double fertilisation" which is probably of universal occurrence in Angiosperms. In *Capsella* fusion of the polar-nuclei was observed to take place at a very late period, yet division of the fertilised secondary nucleus was sometimes seen to be well-nigh complete while the other antherozoid is still in contact with the nucleus of the oosphere. Division of the ovum occurs after formation of the first four endosperm-nuclei. In *Lepidium* there is a slightly earlier fusion of the polar-nuclei.

But Miss Ethel N. Thomas[1] distingushed herself through being the first to publish an account of the process of "double fertilisation" in Dicotyledons, an undertaking to which she was prompted by Miss Ethel Sargant, who had, by her own original observations, confirmed the work of Nawaschin and Guignard on the Liliaceae. Miss Thomas found that in *Caltha palustris* the two polar-nuclei were usually completely fused before the entrance of the pollen-tube. The generative nuclei when emitted are very minute and are either oblong, or lens,-dumb-bell-, or straight S-shaped. She received the impression that the first generative nucleus emitted was the one which fertilised the polar-nuclei, for the latter process always appeared to be much more advanced than that of the fertilisation of the oosphere, and she suggests that this may partly account for the fact of the phenomenon being overlooked for so long. The vermiform nucleus which fertilises the polar nuclei, increases greatly in size, while this is not the case with the other sperm-nucleus.

The epoch-making experiments on the *hybrid fertilisation of endosperm* conducted by De Vries[2] in 1898 afford a most striking illustration of the reality, and, in certain cases, the far-reaching consequences of the phenomenon of "double fertilisation," this latter, indeed, alone affording an explanation of the facts involved in those experiments. De Vries in 1898 possessed forty specimens of the variety of the Maize-plant whose grains contain a *sugary* endosperm; in the following year he obtained from these grains a second generation of sixty plants producing sixty-seven spikes full of grains all containing sugar only. It is therefore clear that the plants destined for his experiments, being the offspring of the same original lot, would, if fertilised with their own pollen, have yielded pure spikes of sugared grains. The hybrid fertilisation took place in August, 1898. At the beginning of the month, before flowering

[1] "On the Presence of Vermiform Nuclei in a Dicotyledon." — "Double Fertilisation in a Dicotyledon—*Caltha palustris*" (Annals of Botany, Sept. 1902).

[2] "Sur la fécondation hybride de l'endosperme chez le Mais" Revue générale de Bot., vol. xii, 1900).

took place, he cut off the greater part of each male infloresence. On emergence of the stigmas from their bracts he powdered them at intervals with pollen of a variety of Maize possessing grains with *starchy* endosperm, yet without entirely preventing fertilisation by the pollen emanating from the lower branches of their own male inflorescences. The result was ten large spikes full of grains. Each spike bore two kinds of grains, the greater number being starchy like the father, the remainder sugary like the mother. These last were largely due to auto-fertilisation, which was proved by sowing a portion of them in 1899, when they reproduced the sugary variety of the mother. The starchy grains were *hybrids, as well in their endosperms as in their embryos.* The endosperm exhibited entirely the character of the father, being well filled with starch and containing no visible trace of sugar, being a chalky-white within, and having a smooth external surface, without the wrinkles so characteristic of the grains of the sugary variety. It was clear that these paternal characters had been communicated by the second spermatozoid of the pollen-tube. In order to prove the hybrid nature of the *embryos* of these grains he sowed a portion of them in 1899 and allowed the plants to be fertilised by their own pollen. He obtained a crop of thirty-two plants yielding thirty-five spikes, rich in grains All these spikes were of mixed nature, about a quarter of the grains were sugary, the three remaining quarters being starchy ; the former had reverted to the character of the grandmother, the latter exhibited that of the father and grandfather. The starchy grains of his crossed spikes of 1898 were therefore hybrids, capable of reproducing the types of their two parents. In all these spikes there occurred no grains of intermediate character, half sugary, and half starchy.

W. O. Focke, in his great work "Die Pflanzenmischlinge," which contains a résumé of all the experiments conducted by Körnicke, F. Hildebrand and De Vries, proposed the term "xenia" for all cases in which an influence of the pollen on the hereditary characters of the fruit or grain *outside the embryo* has been either determined or presumed. About the same time as, or a little later than De Vries' work, some detailed investigations and experiments were carried out by Correns,[1] as a result of which he established several valuable and important corollaries for which we have no space here. He at first imagined that xenia was due to a fusion of *half the generative nucleus* (as a result of division of the latter) with

[1] "Untersuchungen über die Xenien bei *Zea Mais*" (Berichte der deutsch. bot. Gesellschaft, 1899), etc.

the secondary nucleus of the sac. The process he regards as a case of of true fertilisation inasmuch as the Maize-grain, produced as a result of pollination by another race, contains, besides the bastard-embryo, a bastard-endosperm. A second possible explanation offered by him is that the bastard-embryo exercises an *enzymatic* action on the endosperm, this being not so unlikely, seeing that it is merely a question of formation of colouring-matter or of closely-allied reserve-stuffs It is to be noted that xenia-formation has been observed by Giltay in the Rye, where it corresponds to one of the special cases in the Maize. Correns points out that cases in which races or closely-allied species exhibit essential differences in the character of the endosperm, are, unfortunately, of rare occurrence.

The publication of Nawaschin and Guignard's observations solved the whole problem of xenia or hybrid endosperm-formation, for it is manifest that a fusion of the second male or sperm-nucleus emanating from the pollen of the foreign race with the definitive or secondary nucleus of the embryo-sac, the division of which latter, as we know, invariably gives rise to the endosperm, would supply all the necessary conditions under which a hybrid endosperm could be produced; for just as the fertilised ovum gives rise on division to an embryo combining in itself the characters of the two parents from which the first generative nucleus and that of the oosphere respectively proceeded, precisely the same will be true of the product of division of the definitive nucleus "fertilised" by the second generative nucleus of the pollen-tube.[1]

We have reserved until last the observations or theoretical considerations of the two authors who appear, in our opinion, to shed the brightest light upon this most interesting problem of "double fertilisation." To our thinking Strasburger[2] in this matter maintains his great reputation as a leader in all that concerns investigation into the wonderful developmental history of the embryo-sac. He himself observed "double fertilisation" in several Orchids and in *Monotropa Hypopitys.* He regards the passage through the embryo-sac of the second sperm-nucleus (which, in the plants examined by him, did not always exhibit a worm-like shape) as probably of a *passive* nature. His explanation of the whole course of events in the embryo-sac is as follows:—The prothallus-formation in the embryo-sac of all Angiosperms is divided into two

[1] For an account of Correns' work and its relation to Mendel's laws of hybridism, see THE NEW PHYTOLOGIST, vol. I., 1902, p. 103., *et seq.*

[2] "Einige Bemerkungen zur Frage nach der 'doppelten Befruchtung' bei den Angiospermen" (Botanische Zeitung, 1900).

distinct stages,[1] the first stage consists in the formation of the synergids and antipodal cells; after the third division, resulting in the production of the eight nuclei in the sac, these latter no longer possess the power of dividing further; hence an interruption in the process of prothallus-formation, during which interval fertilisation of the ovum takes place. But it can be readily seen that, should this latter function fail to be performed, the formation of endosperm (prothallus) would entail a great waste of energy, hence we find that in the vast majority of cases the latter is made *dependent on the former*. But, and here we reach the core of the whole problem, inauguration of the second stage of prothallus-formation must be effected by some *fresh stimulus*; and this is afforded by the second sperm-nucleus, which, through fusion with the definitive nucleus of the sac, increases the nuclear substance of the latter, inducing thereby the divisions which constitute the second stage of prothallus- or endosperm-formation to proceed rapidly. The interesting results obtained in Maize-cultures, which led Correns to entertain the mistaken idea that this "double fertilisation" constituted a process of true fertilization, could hardly have been different when fusion between the sperm and the definitive nucleus takes place.

The whole character of the endosperm is antagonistic to the idea of its being a second "nutritive embryo." Yet he suggests that the process which now consists merely in a stimulus may in the course of time have been degraded from a process of true fertilisation.

Strasburger cites cases where, *in the absence of fertilisation*, the formation of endosperm may take place, *e.g.*, in *Cœlebogyne* (where adventitious embryos occur), *Ranunculus multifidus*, *Antennaria alpina* (in which each polar-nucleus divides independently), and *Balanophora elongata* (in which the *upper polar-nucleus only* divides). He mentions that these cases may possibly represent reversions to the time when the sac became filled with a prothallus before fertilisation.

Celakovsky,[2] the great Bohemian morphologist, adheres to the view put forward by Strasburger[3] that the production of endosperm is "*a continuation of the original process of endosperm-formation which had been interrupted by the early appearance of fertilisation*, all the

1 This view had also been expressed by Guignard in his early work on the embryo-sac.

2 "Ueber den phylogenetischen Entwickelungsgang der Blüthe, &c.," Part II., p. 207 (Sitzungsberichte der königl. böhm. Gesellschaft der Wissenschaften in Prag, 1900).

3 Die Angiospermen and die Gymnospermen, 1879.

original nuclei of the sac corresponding to the prothallus, along with archegonia, in the Gymnosperms. This idea of a retarded prothallus-formation is confirmed by Karsten's observations on species of *Gnetum* in which a similar phenomenon occurs; but in these cases many free nuclei of the endosperm arise before fertilisation, while in Angiosperms only two such free nuclei (the polar nuclei) are present. In *Gnetum Gnemon*, where an abundant endosperm is developed in the lower part of the embryo-sac before fertilisation, the *later-formed* rudimentary endosperm aborts, while in the Angiosperms, on the contrary, this is what happens to the reduced *primary* endosperm, while the later-formed endosperm persists. In view, therefore, of the fact that the secondary persistent endosperm of Angiosperms is the homologue of the secondary aborting endosperm of *Gnetum Gnemon*, and that there can be no possible question of the latter partaking of the nature of an embryo, it follows that the former also can never be identified with an embryo, and *cannot therefore correspond to the second zygote* [*the product of fertilisation*] *of Gnetum Gnemon*.[1]

As regards the activities of the second sperm-nucleus, Celakovsky points out that if this latter fused *merely* with the sister-nucleus of the ovum, *viz.*, the upper polar-nucleus, the product of fusion could hardly be regarded in any other light than as a twin-product with the egg. But the idea of a true sexual act in connection with the process which actually does occur, *viz.*, fusion with the product of union of both polar-nuclei, is not to be entirely rejected. The first thing to discover is what this "double-nucleus" with which the sperm-nucleus has united really is, and especially to what *cell* it belongs. *The cell-nucleus of the megaspore* or embryo-sac, having been resolved into its posterity of eight nuclei, becomes, through fusion of the polar-nuclei, *regenerated*, and its original energy restored, this being necessary in order that there might be a rapid continuation of the cell-formation which, begun by the primary embryo-sac nucleus, had later been interrupted. This secondary nucleus also assumes once more the position in the centre of the sac which had previously been occupied by the primary nucleus. On this hypothesis the endosperm is *not a sister-product or twin with the embryo*, but the retarded portion of the mother-structure: the prothallus. Inasmuch as a sperm-nucleus fuses with the polar-nuclei it must be assumed that these latter have assumed an actual female character, for otherwise the attraction of the male nucleus

[1] See Lotsy's work on *Gnetum Gnemon*.

to the same would be, in the light of our present knowledge, incomprehensible. "The influence of the male nucleus on the fusing polar-nuclei is probably a necessary factor in the case, consisting in a stimulation of the female double-nucleus to further activity, by affording it a renewed supply of energy, while at the same time, as the experiments with the Maize appear to shew, characters from the male side are inevitably transferred to the regenerated megaspore-nucleus," Celaskovsky states finally that he cannot admit that the originally normal process of fertilisation, the product of which is an embryo, has become *degraded* to a process of mere pseudo-fertilisation and the embryo to an endosperm-thallus, but must regard *the new sexual act as phylogenetically an advanced process ("Höherbildung")*; for the original asexually-formed prothallus (in Pteridophytes, Gymnosperms, and possibly in many Angiosperms) becomes, in its second retarded stage (as in the case of certain, if not all, Angiosperms), sexually produced like the embryo.

To our own mind, and as far as we can judge, the view set forth by Celakovsky affords a quite satisfactory solution of the whole problem; it is nevertheless desirable that further observations of fact should be forthcoming.

W. C. W.

ON ASEXUAL REPRODUCTION AND REGENERATION IN HEPATICAE,

By F. Cavers,

Yorkshire College, Leeds.

(With Eight Figures in the Text).

(*Continued from page* 133.)

Gemmae. In the Acrogynae the gemmae, which are usually unicellular or few-celled, are formed from the cells of the leaf and sometimes also from the superficial cells of the stem. Not only the ordinary lateral or foliage leaves, but the amphigastria, the male and female bracts ("perigonial" and "involucral" leaves), and even the perianth may bear gemmae. The process of gemma-formation may be confined to the margin of the leaf or to the tips of the lobes in a divided leaf, or it may encroach more and more upon the tissue of the leaf, until the latter is represented only by a cluster of loosely-connected gemmae. In a considerable number of forms (*e.g.*, *Cephalozia bicuspidate*, *Kantia trichomanis*), the apex

of the main stem or of its branches often becomes entirely given over to the production of a rounded mass of gemmae; these gemmiferous shoots often grow erect and assume apparently radial symmetry, the amphigastria becoming here similar in form to the lateral leaves and like them producing strings or clusters of gemmae, whilst the shoot is terminated by a globular mass consisting of branched rows of gemmae (Fig. 6).

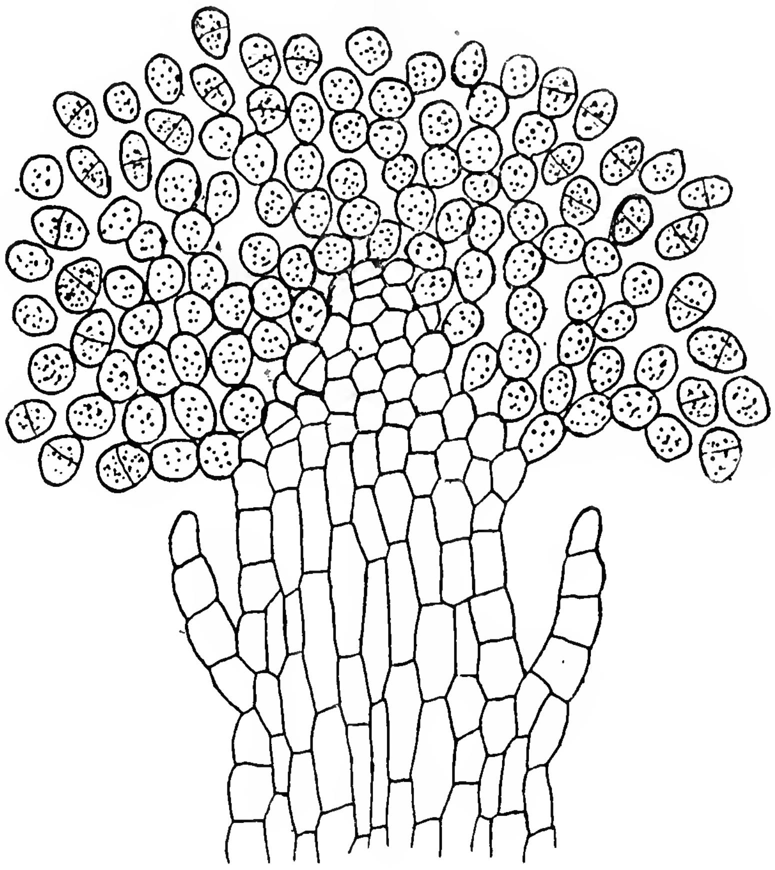

Fig. 6. *Cephalozia bicuspidata.* Longitudinal section through the apex of an erect gemmiferous shoot, showing two of the reduced leaves and numerous gemmae, some arranged in branching chains. × 150.

The gemmae may be either (1) uni- or bi-cellular bodies, formed singly or in chains and branched clusters on the margins of the leaves or the summit of the stem; or (2) discoid multicellular bodies arising on the margins or the surfaces of the leaves.

The uni- or bi-cellular gemmae are usually spherical or ovoid in form (Fig. 6), but sometimes they are tetrahedral (*e.g.*, *Lophozia ventricosa*) or polygonal [*e.g.*, *Diplophyllum albicans* (Fig. 7)]. In most cases they are green or yellowish in colour, but frequently they are red, brown, or purple (*e.g.*, *Scapania nemorosa*).

Discoid gemmae occur in the families Stephaninoideae (*Radula*), Bellincinioideae (*Porella*), and Jubuloideae (*Frullania*, *Lejeunea*); whilst uni- or bi-cellular gemmae are found in all the remaining families, except the Pleurozioideae (*Pleurozia*). Gemmiferous species occur in the great majority of the Acrogynous genera, and it would appear that the production of gemmae plays

an important part in the propagation of these plants, especially in the case of species which are seldom found in fruit.

In the subjoined list, the principal characters of the gemmae are briefly noted. Except where otherwise stated, the species occur in the British Islands, the families being given in accordance with the system proposed by Spruce[1] and adoped by Schiffner.[2]

Fam. I. *Epigonianthcae*. *Marsupella emarginata*. Gemmae ovoid, 1-2-celled, pale brown, on leaf-margins, especially those near top of stem.

Lophozia barbata, *L. intermedia*, *L. orcadensis*, *L. porphyroleuca*, *L. ventricosa*. G. triangular or polygonal, 2-3-celled, in brown masses on tips of uppermost leaves.

L. exsecta, *L. Helleriana*. G. ovoid, 1-3-celled in dark-red masses on uppermost leaves "In *L. exsectaeformis*, however, the gemmae are triangular and 1-celled."

L. heterocolpa. G. ovoid, 1-2-celled, in a large reddish mass at stem-apex, surrounded by uppermost leaves.

L. incisa. G. polygonal, 1-celled, in yellowish masses on the crowded terminal leaves.

L. minuta. G. ovoid, 1-celled, in small brown masses on the leaves of special slender shoots.

Lophocolea bidentata, *L. heterophylla*. G. occur either as isolated spherical or ovoid cells on leaf-margins, or as irregular masses on the upper leaves and the tops of erect shoots.

Mylia Taylori, *M. anomala*. G. ovoid or elongated, 1-2-celled, in dark-green masses on uppermost leaves, singly on the lower ones.

Fam. 2. *Trigonantheae*. *Cephalozia bicuspidata*, *C. catenulata*, *C. dentata*, *C. divaricata*. G. spherical or ovoid, 1-2-celled, in light-green masses on the summit of erect shoots, and on margins of uppermost leaves (Fig. 6).

C. Francisci. G. triangular, 2-celled, in reddish masses on the tips of the uppermost leaves of slender shoots.

C. Starkii. G. ovoid, 1-2-celled, in brown masses on tips of upper leaves.

Nowellia curvifolia. G. spherical, 1-celled, scattered on margins of upper leaves.

Odontoschisma Sphagni, *O. denudatum*. G. spherical or ovoid, 1-2-celled, in masses at the ends of slender small-leaved branches.

[1] Spruce, R., Hepaticae Amazonicae et Andinae. Trans. Bot. Soc., Edinburgh, Vol. 15. 1885.

[2] Schiffner, V., Hepaticae. Engler u. Prantl, Nat. Pflanzenfamiiien, Teil. 1, Abt. 3, 1893.

Kantia trichomanis, K. suecica, K. submersa. G. spherical or ovoid, 2-celled, in a large globular green mass at the summit of an erect shoot, also scattered on the upper leaves and amphigastria.

Fam. 3. *Ptilidioideae. Ptilidium ciliare.* G. spherical or ovoid, 1-2-celled, scattered on the margins of the leaves, especially the uppermost ones.

Blepharostoma trichophyllum. G. spherical, 1-2-celled, formed in chains from the segments of the much-divided leaves, especially those near summit of shoot.

Trichocolea tomentella. G. as in *Blepharostoma.*

Fam. 4. *Scapanioideae. Scapania aequiloba, S. aspera, S. Bartlingii.* G. ovoid, 1-2-celled, in dark-green masses on margins of uppermost leaves.

S. compacta, S. umbrosa G. elongated, 1-3-celled, in radiating chains forming a rounded yellowish mass at summit of stem, surrounded by the uppermost leaves.

S. crassiretis. G. ovoid, 1-celled, in brown masses on uppermost leaves.

S. irrigua, S. undulata. G. ovoid, 1-3-celled, in rounded light-green masses at the stem-apex, also scattered on uppermost leaves.

S. nemorosa. G. ovoid, 1-3-celled, in dark-brown masses on the tips of the upper leaves, sometimes also in a ball at the stem-apex.

S. resupinata. G. ovoid, 1-3-celled, in a reddish-brown ball at the stem-apex, also scattered on margins of uppermost leaves.

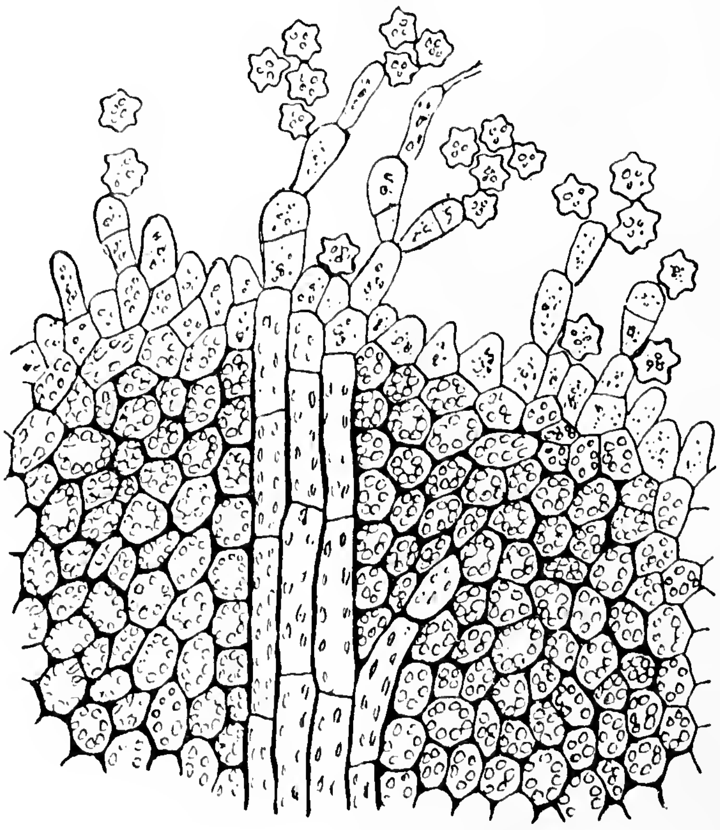

Fig. 7. *Diplophyllum albicans.* Upper portion of a leaf, showing formation of numerous small polygonal gemmae from the marginal cells. × 150.

Diplophyllum albicans. G. polygonal, 1-celled, in yellowish clusters on the leaf-margin, towards the tips of the smaller upper and the larger lower lobes. Both the elongated cells of the "midrib" and the polygonal cells on each side of this take part in the production of the gemmae, the leaves often becoming eroded and truncated in consequence (Fig. 7).

Fam. 5. *Stephaninoideae.* In several species of *Radula*, the leaves frequently bear, either on the margin or the lower surface, scattered discoid gemmae, each consisting of a plate of cells, circular or oval in outline. The writer has followed the development of the gemmae in *R. complanata.* Each gemma arises from a single marginal cell, which grows in size and becomes further distinguished from the cells on either side by containing from one to four small brown oil-bodies, in addition to the large oil-body normally found in each of the leaf-cells in this species. These extra oil-bodies do not appear to arise by division or budding from the larger one, but are developed independently by segregation of the protoplasm to form a stroma, in which oil-drops soon appear. The cell then undergoes repeated divisions, the small oil-bodies passing into the newly-formed cells, so that ultimately each cell of the gemma contains one of these bodies, which becomes enlarged until it reaches about the same size as the oil body of the ordinary leaf-cell. The gemma is attached to the leaf-margin by a narrow base consisting of one or two cells, and shows on its distal margin a large apical cell, triangular in surface view, from which the young leafy shoot arises, when the gemma becomes detached and begins to germinate. Similar gemmae are found in *R. germana* and *R. Lindbergii*, which occur in Britain. In some tropical species of *Radula*, *e.g.*, *R. tjibodensis*, the gemmae are larger than in *R. complanata*, and some of the marginal cells are modified to form organs of attachment, regarded by Goebel[1] as rhizoids of arrested growth, by which the gemma fixes itself to the substratum (leaves and trunks of trees).

Fam. 6. *Pleurozioideae.* In this family, represented by the single genus *Pleurozia (Physiotium)*, gemmae do not appear to have been yet observed.

Fam. 7. *Bellincinioideae.* In *Porella rotundifolia*, from Brazil, Schiffner[2] figures discoid gemmae on the lower surface of the leaf, evidently resembling those of *Radula* and various Lejeuneae.

[1] Goebel, K., Epiphytische Farne und Muscineen. Ann. du jard. bot. de Buitenzorg, Vol. 7, 1887.

[2] Schiffner, V., Ueber exotische Hepaticae; Taf. 6, Fig. 2.

Fam. 8. *Jubuloideae.* In *Frullania dilatata*, gemmae are sometimes formed on the margins of the leaves, each consisting of four to six cells as a rule and being discoid or irregular in form. The outer surface of the perianth in this species bears numerous irregular outgrowths, each made up from two to five or six cells. These outgrowths may be regarded as gemmae, for the writer has found that when the whole or a portion of a perianth is isolated and kept under cultivation, some of them give rise to leafy shoots, either before or after becoming detached from the perianth. The caducous lobules of *F. fragilifolia* have already been described under the heading of adventive shoots, but these organs might reasonably be regarded as gemmae, since they become detached from the plant before giving rise to the new leafy shoot. In several of the Lejeuneae, there are produced discoid gemmae, similar to those of *Radula* in general form, but in some cases showing peculiar features. In *Thallolejeunea (Metzgeriopsis) pusilla*, a remarkable form discovered in Java by Goebel,[1] the vegetative portion of the plant consists of a repeatedly-branched thallus with toothed margins, whilst the sexual organs are borne on short leafy shoots each arising from the apex of a branch. The thallus bears on its upper surface and its margins numerous discoid gemmae, each consisting of an oval plate of cells, lying parallel with the surface of the thallus, to which it is attached by a short stalk-cell. The mature gemma consists of about twenty cells, arranged in a single layer, and shows two growing-points occupying opposite sides of the gemma and each showing a wedge-shaped apical cell. Similar gemmae are also found on the male and female bracts.

Discoid gemmae are formed on the leaves of *Cololejeunea calcarea* (Fig. 8), *C. minutissima*, *C. microscopea*, *Eulejeunea serpyllifolia*, and *Colurolejeunea calyptrifolia*, all of which occur in Britain. In some tropical forms described by Goebel, *e.g.*, *Cololejeunea Goebelii*, *Odontolejeunea mirabilis*, the gemmae have two growing-points, as in *Metzgeriopsis*, and some of the marginal cells are modified to form organs of attachment. The writer has followed the development of the gemmae in *Cololejeunea calcarea* (Fig. 8), which are sometimes found in abundance on the lower surfaces of the leaves, each consisting when mature of a circular or oval disc, one cell in thickness, attached to the leaf by a single stalk-cell which is inserted at the centre of the lower surface of the gemma.

[1] Loc. cit., p. 54, Tab. 6—8; also Schiffner, V., Morphologie und systematische Stellung von *Metzgeriopsis pusilla*. Oesterr. botan. Zeitschrift, 1893, p. 4 of reprint.

The gemmae are formed on both the larger upper lobe and the smaller lower lobe of the leaf; the two lobes are sharply folded on each other, so as to form a kind of pocket, in which the writer frequently found a number of free gemmae. Probably the gemmae, on becoming loosened from their unicellular stalks, which usually

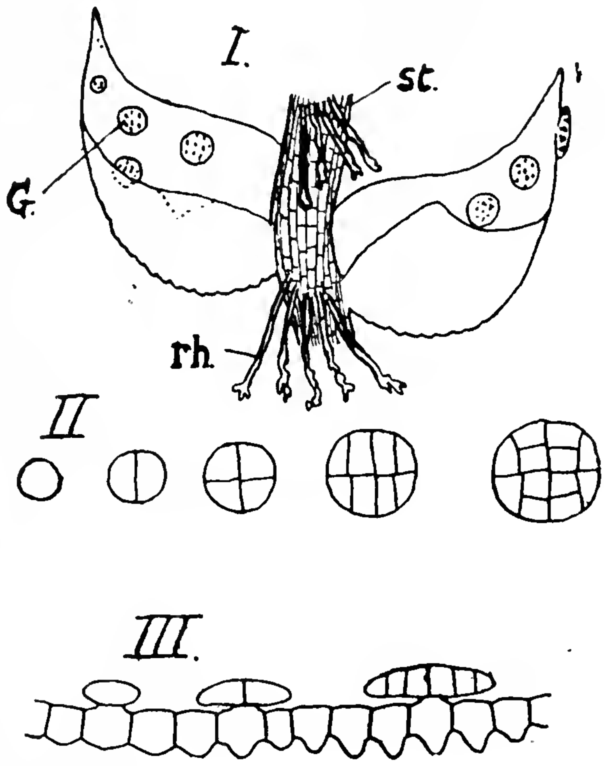

Fig. 8. *Cololejeunea calcarea.* I. Part of a plant, seen from ventral surface, showing two leaves with gemmae (G.): *st.*, stem; *rh.*, rhizoids. × 30. II. Stages in development of gemma, as seen in surface view. × 100. III. Part of leaf in vertical section, showing three developing gemmae. × 100.

remain behind and mark the spots where gemmae have been formed, accumulate in the basal pocket of the leaf, from which they may ultimately be washed out by rain-drops. In a few cases, these free gemmae had already begun to germinate within the basal sac. The cell-divisions in the developing gemma show great regularity (Fig. 8, II., III.), the marginal cells being all of nearly the same size, so that here there does not appear to be any definite growing-point in the mature gemma, as in *C. Goebelii*, but the young shoot may arise from any one of the marginal cells.

III. *Anthocerotales.* In *Anthoceros laevis*, adventive branches are sometimes formed, each arising from a single superficial cell of the thallus. The occurrence of gemmae has been described in *A. glandulosus* and in some species of *Dendroceros (D. cichoraceus, D. javanicus)*. In *Dendroceros*, the gemmae are small rounded or irregular bodies, each formed from a single cell of the thin wings or leaves. In *Anthoceros glandulosus*, Ruge[1] found that each gemma arose as a club-shaped outgrowth from a superficial cell, which

[1] Ruge, G., Beiträge zur Kenntniss der Vegetationsorgane der Lebermoose, Flora, 1893, Heft 4; p. 36 of reprint.

divided repeatedly by transverse walls, giving rise to a row of cells. The uppermost cell then became enlarged and divided by a longitudinal wall. Repeated transverse and longitudinal divisions then occurred in this swollen terminal portion, in the interior of which an intercellular space was formed by splitting of the primary longitudinal wall. This closed sac then became filled with mucilage, whilst two other mucilage-cavities were also formed immediately above the insertion of the stalk of the gemma, but each of these opened externally by a slit and resembled the ordinary *Nostoc*-cavities of the thallus. The tubers which have been described in various exotic species of *Anthoceros*, and more recently by Goebel[1] in *A. laevis* itself, may be regarded as organs of asexual propagation, especially when several tubers are borne on one plant. These tubers, as in the case of *Riccia*, *Fossombronia*, *Geothallus*, and *Petalophyllum*, arise as swellings on the lower surface of the thallus, near the margin; their cells contain reserve food-materials, and they are adapted for carrying the plant over unfavourable climatic periods and of germinating to form new plants.

Regeneration of the Gametophyte.

Necker appears to have been the first to describe the process of gametophytic regeneration in Hepaticae. In his "Physiologia Muscorum," published in 1774, he states (p. 27) that he cut the thallus of *Marchantia polymorpha* and of *Fegatella conica* into numerous small pieces, which he cultivated on soil and watered daily. In about a month, he observed outgrowths arising from many of the fragments, each outgrowth at length giving rise to a new plant. He obtained similar results in his experiments with *Ricciella fluitans* and with a number of leafy Jungermanniales These observations of Necker's appear to have been entirely overlooked by later writers on the subject.

In 1885 Vöchting[2] published an important paper in which he showed that the gametophyte of *Lunularia* and *Marchantia* possesses in an extraordinary degree the property of regeneration. On cutting out portions of the thallus or of the sexual receptacles and keeping them under cultivation, he obtained numerous adventive outgrowths, each arising from a single cell. Even when portions of the thallus were minced up into very small fragments, many of the latter were found to give rise to new shoots. Vöchting therefore concluded that in the gametophyte of these Liverworts, every cell

[1] Goebel, K., Organographie der Pflanzen, p. 294.

[2] Vöchting, H., Ueber die Regeneration der Marchantieen. Jahrb. für wiss. Botanik, Band 16, Heft 3, 1885.

is capable of regenerating the entire plant, provided that it retains its living protoplasmic contents and is exposed to favourable conditions. As already stated, naturally-occuring adventive outgrowths have been observed on the female receptacles of *Marchantia* and *Dumortiera*, but such intances of regeneration in the specialised sexual shoots of the Marchantioideae are extremely rare in nature, though the formation of adventive shoots is readily induced when the antheridiophores or archegoniophores, or portions of these, are severed from the rest of the plant and kept under cultivation. Schostakowitsch[1] has confirmed and extended the observations of Vöchting. He obtained adventive growths from cultures of excised portions of the thallus in *Riccia crystallina*, *Ricciella fluitans*, *Riccioearpus natans*, *Corsinia marchantioides*, *Fegatella conica*, *Preissia commutata*, and *Anthoceros laevis*, also from isolated leaves or leaf-fragments in *Haplomitrium Hookeri*, *Plagiochila asplenioides*, *Lophocolea bidentata*, *Chiloscyphus polyanthus*, *Lophozia Mulleri*, *Porella platyphylla*, *Frullania dilatata*, and *Lejeunea serpyllifolia*. To the cases observed by the writers mentioned, the writer can add the following, in which adventive shoots were formed as the result of cultivating severed thallus-or leaf-fragments on damp sand or filter-paper:—*Riccia glauca*, *Reboulia hemispherica*, *Aneura multifida*, *A. pinnatifida*, *A. latifrons*, *A. pinguis*, *Pellia epiphylla*, *P. calycina*, *Monoclea Forsteri*, *Cephalozia bicuspidata*, *Lepidozia reptans*, *Scapania undulata*, *S. nemorosa*, *Diplophyllum albicans*, *Radula complanata*. In *Riccia* and *Reboulia*, the new shoots were found to arise from the dorsal chlorophyll-bearing tissue as well as from the ventral colourless tissue of the thallus-fragments. This was found by Schostakowitsch to be the case in *Corsinia*, though he states that in *Riccia crystallina* the new growths proceeded only from the ventral surface of the midrib.

In addition to the important generalisation proposed by Vöchting, namely, that in practically every living cell of the Liverwort-gametophyte there resides a latent capacity for regenerating the entire shoot, some other interesting results have been arrived at by the observations of Goebel and Schostakowitsch. Goebel[2] has shown that, at any rate in the Jungermanniales, the

[1] Schostakowitsch, W., Ueber die Reproductions-und Regenerationserscheinungen bei den Lebermoose. Flora, 1894 (Erg.-Bd.), pp. 350—384.

[2] Goebel, K., Ueber die Jugendzustände der Pflanzen. Flora, 1889, p. 15; Ueber die Jugendformen von Pflanzen und deren kunstliche Wiederhervorrufung. Sitz.-Ber. d. Kais. Bayer. Akad., 1897.

young shoot arising from a germinating gemma is formed in exactly the same manner as that proceeding from a germinating spore of the same species. In the majoritiy of the leafy forms, the germinating gemma, like the germinating spore, usually gives rise to a "germ-tube," a slender filament at the distal end of which the young leafy shoot is developed. On the other hand, in *Aneura*, *Radula*, *Frullania*, and the Lejeuneae, the formation of a germ-tube is suppressed; the germinating spore or gemma of *Aneura* gives rise to a flattened ribbon-like outgrowth, the distal end of which is from the first occupied by the two-sided apical cell of the shoot, whilst in *Frullania*, *Radula*, and the Lejeuneae, the gemma exactly resembles the protonema arising from the spore, forming a discoid cell-mass, from the margin of which the leafy shoot takes its origin.

As regards the influence of external conditions on the formation of adventive shoots from excised portions of the Liverwort-gametophyte, the writer has found that, both in the thalloid and the foliose forms investigated, regeneration takes place in darkness as well as in light, but that the shoots formed in the dark show only feeble growth. This was observed in *Reboulia hemispherica*, *Preissia commutata*, *Marchantia polymorpha*, *Lunularia cruciata*, *Fegatella conica*, *Pellia epiphylla*, *Lophocolea bidentata*, and *Scapania undulata*; a similar result was obtained by Heald[1] in the case of *Lophocolea*. Schostakowitsch was unable to obtain regeneration in cultures of severed leaves of various Jungermanniales which he kept in darkness, though Klebs[2] found that in *Lophocolea* the leaves produced new shoots from the marginal cells when placed in weak light, whilst spores grown under similar light-conditions produced germ-tubes but no leafy shoots. Schostakowitsch found that no regeneration occurred in detached leaves which were cultivated in air deprived of CO_2, and concluded from this negative result that light does not exert a specific influence on the regeneration-processes, which failed to take place in this case on account of the lack of plastic food-materials.

Apospory.

Apospory, or direct origin of the gametophyte from the vegetative tissue of the sporogonium without the intervention of the spore itself, has been observed to take place in a number of Mosses, when the sporogonium has been detached and cultivated in

[1] Heald, F. de F., Gametophytic Regeneration as exhibited by Mosses, etc. Inaug.-Diss., Leipzig, 1897, p. 21.

[2] Klebs, G., Ueber den Einfluss des Lichtes auf die Fortpflanzung der Gewächse. Biol. Centralblatt, Band. 13, 1893, p. 649.

fragments or entire (*Ceratodon purpureus, Hypnum cupressiforme, H. molluscum, Amblystegium serpens, Bryum caespiticium*), or even whilst the sporogonium remains attached to the Moss-plant (*Funaria hygrometrica*).[1] Lang[2] has recently shown that apospory occurs in *Anthoceros laevis.* He found that on cutting up the sporogonia and laying them on damp sand, green outgrowths arose from the surfaces and cut ends of the fragments. These outgrowths frequently bore rhizoids and strongly resembled the young plants formed from germinating spores. Sections showed that these shoots were usually developed from the hypodermal layer s of the capsule, and that each arose from a single cell.

The writer has made numerous cultures with a view to ascertaining whether this phenomenon occurs in other Hepaticae. Young capsules of *Pellia epiphylla*, *P. calycina*, *Fegatella conica*, and *Lophocolea bidentata*, were dissected out and portions of the seta and of the capsule-wall (in the latter case the spore mother cells or the young spores were as far as possible removed by means of a camel-hair brush) were grown on damp sand. In no case, however, was any outgrowth observed; the cells grew in size, and, in the case of the pieces of capsule-wall, remained green for some weeks, but ultimately became withered and discoloured. The writer hopes, however, to resume the search in the autumn, when young sporogonia are again available, for in view of Lang's discovery of apospory in *Anthoceros*, there seems to be a strong probability that this phenomenon may be induced in other forms, especially as in most cases the cells forming the wall of the young capsule contain abundant chlorophyll, which is at a later stage lost, together with the other cell-contents, when the formation of ring-thickenings takes place.

In conclusion, the writer desires to acknowledge his obligations to the following gentlemen, who have generously sent him material, in many cases consisting of living plants:—Mr. P. Furley, Aberystwyth; Mr. W. Ingham, York; Mr. J. H. Mitchell, Bradford; Mr. W. H. Pearson, Manchester; Mr. M. B. Slater, Malton; and Mr. G. Webster, York.

1 Correns, C., Untersuchungen über die Vermehrung der Laubmoose, 1899, p. 421, and papers by Stahl, Pringsheim and Brizi, there cited.

2 Lang, W. H., On Apospory in *Anthoceros laevis.* Annals of Botany. Vol. 15, 1901, p. 503.

THE facts of mitosis have been studied, to a greater or less extent, in almost all the great groups of the vegetable kingdom. The mosses, however, form a notable exception to this statement. This neglect is probably due, partly to the small size of the nuclei in these plants, and partly to the technical difficulties which have to be surmounted.

When we recollect the interesting results which the study of the cytology of the neighbouring group of liverworts has yielded in the hands of Prof. J. B. Farmer it appears all the more desirable that an effort should be made to trace the processes of mitosis in the Musci even in the face of the difficulties which are presented.

In the present note I wish to call attention to a rough but simple method by which the distribution and number of the chromosomes in the dividing cells can be studied with the greatest ease. Whilst examining the behaviour of the spore-mother-cell wall of *Funaria hygrometrica* toward different reagents I teased out a preparation of spore mother-cells into a physiological salt solution in which the living and unaltered cell could be studied. It could be obscurely seen that the nuclei of the mother-cells were undergoing mitotic division and with care it was even possible, dimly to make out the chromosomes. I now ran a little 1% solution of KOH containing a trace of Congo-red under the cover glass. Immediately the chromosomes, which before could only be indistinctly seen, stood out with remarkable clearness. By this means it was possible not only to follow their distribution but also to ascertain their number with absolute certainty.

The centre of the dividing spore mother-cell is seen to be occupied by four, comparatively long, rod-shaped chromosomes. By the division of these bodies eight daughter-chromosomes are formed and these separate from one another in two groups so that four daughter-chromosomes travel to each pole. Whether these immediately split again to form the chromosomes of the special mother-cells or whether the daughter-nuclei are first reconstructed, was not followed in these preparations. The appearance of both mother and daughter-chromosomes, which have been subjected to this treatment, is coarsely and irregularly granular. An examination of properly fixed capsules of *Funaria* by means of the more approved methods of microtechnique is in progress and I hope before long to describe some of the cytological features in the development of the spores of this plant in greater detail.

RUDOLF BEER.

AN EXPERIMENT IN ECOLOGICAL SURVEYING.

It may be of interest to many of our readers to know of an experiment in ecological surveying by a number of advanced students, recently carried out by the Botanical Department of University College, London.

The locality chosen was Eastern Norfolk. Here, in the well-known "Broad" region, one has comparatively large stretches of undrained marsh, bordering on the shallow lakes or Broads and the rivers with which they are connected. In places these marshes pass gradually into the adjacent Broads, which tend to be filled up by the invasion of the marsh-plants if they are not kept clear by dredging and reed-cutting. These marshes are practically at sea-level, and in some places, where they approach very near to the coast, they are only separated from the sea by a barrier of blown sand. This sand forms typical dunes bearing the regular sand-flora for considerable stretches of coast. On the land side the sand is blown over the fresh-water marsh in a thin layer, and here the flora is transitional between sand and marsh.

Thus there exists in E. Norfolk both freshwater and sand floras largely undisturbed by cultivation, so that the natural "associations" or communities of plants are well seen.

The method adopted on the recent expedition was first to familiarise the members of the party with the type of scenery and the constitution of the marsh and water flora by sailing through a part of the country, visiting the marshes and collecting at intervals; afterwards two or three days were spent in a selected limited area which shewed a more or less typical development of the marsh and water associations. During the whole time the party lived and worked on two yachts, which formed a very satisfactory mobile base. Finally two days were spent in examining the flora of the sand dunes on a part of the coast.

Collections as complete as possible were made of the plants on the areas specially studied, the different "associations" were recognised and their boundaries approximately traced, or, in other cases, "sections" were made through the area in a direction transverse to the "strike" of the formations, the inclination of the ground, if any, the character of the soil, the water-level, and the dominant and subordinate species being noted at different points of the section. An interesting section was in this way made for instance through the "rand" or undrained marsh bordering on one of the

Broads, and continued across the end of the (largely grown-up) Broad itself, soundings, and samples of the bottom-vegetation being taken every few feet. Facilities were most kindly given by the local landowner for carrying out this survey. Other sections were taken from high tide-mark across the dunes, shewing the gradual change in the flora from "white" to "grey" dunes.

The surveying was done on tracings taken from the $\frac{1}{2500}$ Ordnance Survey Maps. This large scale was found necessary to shew the local variations of the vegetation.

Though considerably less was actually accomplished than had been planned, the expedition may be said to have been very successful. Some interesting data were obtained, and there is no doubt that the main object, to bring the members of the party into intimate contact with these extensive and practically untouched "plant-communities" was fully realised. It is intended to continue the work in the future, as opportunity offers.

BOTANICAL PHOTOGRAPHS.

Mr. Alfred W. Dennis, of 45, Park Street, Stoke Newington, has a collection of photographs of British Plants in the form of lantern slides, to which he is adding as opportunity offers. Most of them are very successful portraits. In the case of trees a flowering and fruiting shoot has usually been photographed, while the small plants are taken in their entirety. The price is one shilling each.

R. Madley, Printer, 151, Whitfield Street, W.

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THE SOUTHPORT MEETING OF THE BRITISH ASSOCIATION.

THE British Association Meeting at Southport (Sept. 9th to 17th), in spite of the comparatively slight attractions presented to scientific visitors by the town and neighbourhood, drew a more numerous attendance than many of the meetings of recent years, and much of the sectional work seems to have been of a high standard.

To the botanist the most attractive feature of Southport is the magnificent stretch of sand dunes extending southward to the Mersey estuary. Not only are the general characters of sand-dune vegetation beautifully illustrated, but there are some exceptionally interesting ecological features as well as a number of uncommon species.

The housing of Section K in the Chapel Street Church Schoolrooms was entirely satisfactory. The actual meeting-room was large and comfortable, with a small well-raised platform and an excellent lantern screen and frame for holding diagrams. The local Secretary, Mr. Henry Ball, gave every assistance to the other officers, and his hearty goodwill materially contributed to the successful working of the section.

Three distinguished foreign botanists, Dr. Lotsy of Leiden, the general editor of the *Botanisches Centralblatt*, Professor Lignier of Caen, and Professor Atkinson of Cornell, attended the meetings of the Section.

There was a very full programme, the section sitting every morning and afternoon with the exception of Saturday, which was spent in excursions. Two mornings were devoted to general presentations of particular topics by means of the reading of several cognate papers specially prepared to supplement one another, followed by a discussion. This feature certainly gives more scientific interest to the sectional meetings than is obtained when all the

meetings are taken up with the reading of miscellaneous papers, even if these are grouped according to branches of the science, as has been the custom for some years.

President's Address to Section K.

The President, Mr. Seward, took the very wise course of devoting his Address to a topic on which he is a recognised authority, and while maintaining the tradition of making a wide survey and drawing together a number of scattered facts, produced a really valuable contribution to his branch of science. As Professor Balfour said in moving the vote of thanks, the delivery of this address marks a distinct step in the progress of Palæobotany.

The general subject of the address was "the geographical distribution of the floras of the past." We are familiar with outlines of the geological history of the plant-world as it is met with in the north temperate regions, especially in Europe, and with sketches of the geographical distribution of the present-day flora of the earth, but no attempt has hitherto been made to treat the botanical history of the world as a whole. Of course in the present extremely fragmentary state of of our knowledge (not to speak of the imperfection of the geological record), and within the limits of a British Assocation Presidential Address, it is not possible to do more than present the merest outline of this gigantic subject, but Mr. Seward's sketch is none the less of the greatest interest and value.

We cannot in the present notice do more than refer to a very few of the points brought out by Mr. Seward. The general method pursued was to divide the world for the sake of convenience into twenty-two areas, separated horizontally by the limits between the arctic, temperate, sub-tropical and tropical zones, and vertically by arbitrary lines; and then to construct tables, one for each of the well-preserved characteristic floras of the past, in which the occurrence of characteristic fossil types in these different geographical regions is shewn.

In the Devonian and Lower Carboniferous Floras taken together, the preponderance of Pteridophytes, largely of very ancient synthetic types, (the ancestors of our more specialised modern forms), and their world-wide distribution, is clearly brought out, while at the same time the great complexity of their organization plainly indicates the existence of numberless earlier floras representing the simpler stages in the evolution of these highly developed vascular plants, floras of which we have as yet unearthed

no trace, and many of which have almost certainly been lost for ever. In the Upper Carboniferous and Permian epoch we come to an extremely rich flora consisting of Pteridophytes, Cycadofilices and Gymnosperms, which are fortunately sometimes preserved in such a way that their anatomical structure can be investigated. Here also we meet with the extremely interesting fact of the existence of two types of vegetation—a northern and a southern (the so-called *Glossopteris*-flora), which in some areas (*e.g.* Northern Russia, South Africa and Brazil) overlap, but contain for the most part distinct forms. It is probable that while most of the preserved remains of the northern type represent a luxuriant salt-lagoon vegetation, the southern type lived under arctic conditions, as evidenced by the association of the plant–remains with glacial boulder-beds, resting on glaciated rocks. It is probable that this state of things originated by the uniform Devonian and lower Carboniferous flora continuing to flourish in the north, some of its characteristic types being succeeded by new ones, while in the south arctic conditions came to prevail over the huge continental area (the so-called Gondwana Land) of which the present land of the southern hemisphere forms but isolated relics. On this continent the *Glossopteris*-flora originated, and in later Permian and Triassic times "pushed northward over a portion of the area previously occupied by the northern flora."

"During the Triassic period the vegetation of the world gradually changed its character; the balance of power was shifted from the Vascular Cryptogams, the dominant group of the Palæozoic era, to the Gymnosperms." The records are comparatively poor, but there is evidence that while the northern flora was thus changing its character very much, the *Glossopteris*-type persisted in the southern hemisphere.

The Rhætic flora, on the other hand, shows "an almost world-wide range of a vegetation of uniform character. . . . Gymnosperms have ousted Vascular Cryptogams from their position of superiority; ferns indeed are still very abundant, but they have undergone many and striking changes, notably in the much smaller representation of the Marattiaceæ. The Palæozoic Lycopods and Calamites have gone, and in their place we have a wealth of Cycadean and Coniferous types." This new type of vegetation extends with striking uniformity right up to the Wealden (lower Cretaceous) epoch.

The Cycadophyta of this great Mesozoic flora are extremely

numerous and widespread, the few genera existing to-day being but scattered remnants of the great group. In America whole forests of Cycadaceous trees have been found embedded in later Jurassic rocks, while the Cycads of to-day are all found as isolated individuals, usually among the angiospermous trees of tropical or subtropical forests.

The Conifers were largely represented by Araucarioid forms, the recognisable Abietineæ making their mark only in later Mesozoic times.

The Ginkgoales, another phylum of Gymnosperms, of which the Maidenhair-tree (*Ginkgo biloba*) of China and Japan is the sole living representative, were very abundant in all parts of the world.

Among the Ferns, the Polypodiaceæ, which are *the* dominant modern ferns, far more numerous in genera, species and individuals than all the other existing ferns put together, were but slightly represented, though they apparently existed even in Palæozoic times; while other families, now represented by few and isolated forms, *e.g.* Schizæaceæ, Gleicheniaceæ, Dipteridinæ and Matonineæ were widespread and abundant.

The next great flora which we can distinguish is of course that marked by the dominance of Angiosperms, and is the flora which covers the earth at the present time. The sudden rise of this modern flora is one of the most striking phenomena in the geological history of plants. In rocks of the same age as the Wealden beds a few remains of plants which are considered to be Angiosperms have been found, but it is not till later Cretaceous and early Tertiary times that the modern flora appeared in abundance, and then it rapidly secured the supremacy of the plant world. Some of the older types lingered on, but of the lower groups of vascular plants only a few of the ferns (particularly Polypodiaceæ), and some of the Conifers, especially Abietineæ, maintained their hold as the dominant forms over certain areas of the earth's surface.

Mr. Seward's admirable address (which we hope may be reissued in more accessible form) illustrates in a striking way the fundamental fact, whose fuller recognition has been the basis of of the great advances in morphology which have characterised the last decade, that "in every detail the present is built on the past."

After the conclusion of the President's address, the vote of thanks for which was moved by Professor Balfour, and seconded by Dr. Lotsy, the reports of Committees appointed at the last

meeting of the Association were read. The most interesting of these was concerned with the Teaching of Botany in Schools (chairman, Professor Miall of Yorkshire College, Leeds). The Secretary to the Committee, Mr. Wager, gave an admirable summary of the report, in which forcible expression was given to many of the modern ideas on the teaching of scientific subjects to children. The Committee on Botanical Photographs presented a report in which was embodied a scheme for the registration of photographic negatives of botanical interest, such as portraits of British or Foreign plants, photographs illustrating diseases or sports, and photographs shewing natural "plant-associations." A leaflet giving information on the conditions of registrations, etc., has already been widely circulated, and over fifty photographs, of which a considerable number are suitable for registration, have been received. Prints of negatives intended for registration should be sent to the Secretary of the Committee (Professor Weiss, The Owens College, Manchester). The object of the scheme is to draw up a list of registered negatives, so as to inform the students and workers to whom prints or lantern slides of such negatives would be useful of where they may be obtained. The copyright for purposes of publication would of course remain with the owner of the negative. The Committee recommends that negatives intended for registration should, where possible, be of whole or half plate size. This scheme of registration ought to give a stimulus to the systematic photography of our native plant-associations.

At the conclusion of the morning, three papers on Fungi, in the absence of their authors, were read in abstract.

In the afternoon Professor Letts of Belfast, who on more than one previous occasion has brought before the section the subject of the relation of the green seaweeds belonging to the family of Ulvaceæ to sewage effluents, read a paper by himself and Mr. Totton in which he described the appearance of *Ulva latissima* on fragments of brick in the contact-beds used for the purification of Belfast sewage, and of *Enteromorpha compressa* in the effluent collected in a shallow lagoon. The high percentage of chlorine in this sewage supported the view that the algæ obtained entrance to the sewage works by leakage of sea-water. The percentage of nitrogen in the tissue of both the algæ was considerably higher in these conditions than in samples taken from ordinary habitats.

The rest of the afternoon was occupied by a paper by Miss M. C. Stopes on the Colonisation of a Dried River-bed, which is printed

in extenso in the present number of this journal, and by an interesting account, illustrated by lantern-slides, of Mr. A. W. Hill's recent travels in the desert regions of Bolivia and Upper Peru.

Friday morning was devoted to papers on Mendelian heredity. A more or less general account of the principles of the subject, illustrated by his own work on poultry, was given by Mr. Bateson. This was followed by an admirable paper from Miss E. R. Saunders giving the results of her own work in crossing various plants. Finally Mr. C. C. Hurst gave a summary of results obtained from crossing orchids. A few questions were asked and were replied to by the readers of the papers. The interest of Mr. Bateson's and Miss Saunders' papers was much enhanced by their exhibits of specimens of different plants, showing the results of various crossings. The trouble they had taken in selecting and bringing these from Cambridge was much appreciated by the Section.

On Friday afternoon Professor Lignier of Caen read a paper on the flowers of Gnetaceæ, which was criticised by Miss Benson and Dr. Lotsy; Dr. Lotsy followed with an account of the embryo-sac of *Gnetum ula*, in which he shewed that in all probability the embryos in this species are produced from the numerous eggs parthenogenetically.

Dr. Darbishire read a paper on "The Sandhill and Saltmarsh Vegetation of Southport." After giving a short general account of the physical conditions to which sand-dune plants are exposed, he described and illustrated by means of lantern slides the general features of the great sand-dune area lying to the south of Southport. One of the most striking features of this flora is the remarkable abundance of *Salix repens* which forms a pure community over considerable tracts of loose sands and acts as a dune-forming plant. The blown sand lies on the flat surface of peat which borders this part of the Lancashire Coast and in the low lying portions of the dune area the water level rises to near or sometimes above the surface of the soil, so that miniature freshwater marshes are formed in the sand. Here *Parnassia palustris*, *Samolus Valerandi*, etc., flourish; the former with very short peduncles, spangling the ground like daisies on a lawn.

Saturday Excursions.

On Saturday there was a successful Excursion, partly botanical, to the Wirral Peninsula, while a number of the members of

the Section who were particularly interested in coal-measure fossils made an excursion to the famous Dulesgate mine near Todmorden, under the guidance of Mr. Lomax, the well-known preparer of microscopic sections of "coal-balls." The party took train to Todmorden and from there drove up the clough in which the mine is situated. At the entrance of the mine, which is approached by a horizontal gallery not by a vertical shaft, the party was received by the manager. The members were then given lamps and embarked in small square coal trucks of which a train was formed. This train, worked by an endless rope and stationary engine, then slowly proceeded for nearly a mile down a long straight gallery about seven feet high. The recent heavy rains caused cascades of water to pour into the tunnel through cracks in the roof' and by the side of the rails was a torrent. The effect of the rushing water in the darkness of the tunnel was most striking. On getting out of the trucks the party proceeded for some distance further through lower tunnels in which it was impossible to stand up, progress having to be made by stumbling along in a stooping position, often through thick coal-dust mud. The coal seam was four feet thick and near the top of this are found the calcareous nodules or "coal-balls" in which the plant remains are contained. They vary from one to several inches in diameter and are generally somewhat flattened in shape. Many of these were seen *in situ*, and heaps were lying outside the mine.

Monday morning was devoted to a discussion on the Evolution of the Monocotyledons. This was opened by Miss Ethel Sargant, who, in a admirably lucid paper, expounded her theory of their dicotyledonous origin, largely founded on her investigation of the vascular symmetry of Liliaceous seedlings and on that of some of the Ranunculaceæ, particularly the "pseudo-monocotyledonous" forms, but also on certain general considerations, from which the probability of the origin of the monocotyledons by adaptation of their seedlings to the geophilous habit is inferred. Miss E. N. Thomas followed with an account of the available evidence from the development and contents of the embryo-sac bearing on the relation of Monocotyledons to Dicotyledons, The main conclusion was, that, while there is a striking uniformity in this respect throughout the Angiosperms, the monocotyledons have more similarity with the Archichlamydeæ than with the Sympetalæ. This evidence then, while quite compatible with the theory, does not directly support it.

Dr. Rendle followed with a general criticism of Miss Sargant's theory, with which he disagreed on a number of different grounds. Mr. Tansley called attention to two objections, first a point connected with the "double bundles" of the petioles of the cotyledons in the Dicotyledons with which comparison is made, and secondly the unlikelihood of the monocotyledons, plants of the most varied habit and the most primitive of which are not geophilous, being derived from a specialised ecological type like the geophyte. Miss Sargant having replied the discussion closed.

Professor Marshall Ward criticised Professor Eriksson's "Mycoplasm" theory with most destructive effect. Professor Atkinson of Cornell University, created some sensation by stating that he had come straight from Eriksson's laboratory and throwing out dark hints of the latest revelation of discovery there.

In the afternoon Professor Farmer read a most abstruse and learned paper entitled "On Stimulus and Mechanism as Factors of Organisation." This took the place of the usual "semi-popular lecture," a substitution which led to much amusement.

Mr. J. Lloyd Williams followed with an account of his most important work on Alternation of Generations in Dictyotaceæ, an abstract of which appears in the present issue of this journal.

In the evening a most successful botanical dinner was held at the Prince of Wales' Hotel.

On Tuesday morning Dr. F. F. Blackman gave a short account of the historical development of schemes of classification of the Algæ, leading up to the most recent views of Lagerheim, Luther and Bohlin. Professor Marshall Ward gave an interesting little account of the new Botanical Laboratory at Cambridge, illustrated with plans and elevations, and called attention to the distinguishing feature of the new Institute, the attempt to meet the specific wants of the different workers in the Cambridge school of botany.

The President then gave an excellent summary of the leading points of Professor Oliver's and Dr. Scott's recent important work in assigning the fossil seed *Lagenostoma* to the Cycadofilix *Lyginodendron*, with which readers of this journal are already familiar.

Mr. Yapp read a paper on Fruit dispersal in *Adenostemma viscosum*, Mr. Arber on Homœomorphy among Fossil Plants, Mr. T. W. Woodhead on Methods of Mapping Plant Distribution, in which he shewed excellent results in the mapping of the effect of

different types of woodland on undergrowth, and Mr. Parkin on the Localisation of Anthocyan in Foliage Leaves.

In the afternoon there was an excursion to the Sandhills, half the party being conducted by Dr. Darbishire, who demonstrated the leading ecological features of the flora, while the other half followed Mr. Ball, who pointed out some of the rarer plants that inhabit this interesting locality.

Wednesday morning was devoted to miscellaneous papers which we have no space to notice, and this brought the very full and varied work of Section K to a close.

THE USE OF ANATOMICAL CHARACTERS FOR SYSTEMATIC PURPOSES.

THE zoologist will generally hesitate to assign an animal to its systematic position until he has had an opportunity of examining its internal structure and in this branch of biological science the necessity of taking anatomy into account in classification was recognised at an early date. Far later only were the first steps taken towards the use of the anatomy of plants in classification, although here the external morphological differences of closely allied species are often so difficult to detect, that any further distinguishing feature may be welcomed, even though it involve the cutting of a section and its examination under the microscope. Although many earlier authors had indicated the possible value of anatomical characters in classification and others such as Wedell (Monograph of Urticaceae, 1856), had made use of such features, as can be easily detected with the help of a lens (*e.g.*, cystoliths), it was the year 1863 that first saw the publication of a treatise, in which the anatomy of the plant was employed in specific distinction. This is Duval-Jouve's work on the French species of *Equisetum*, which was followed by other papers of the same author and by Bertrand's treatise on the anatomy of the Coniferae and Gnetaceae and ultimately in 1872 by Bureau's work on the Bignoniaceae, in which anatomical features were made use of in the diagnosis of the genera. However Radlkofer's monograph of the Sapindaceous genus *Serjania* is really the first important contribution towards systematic anatomy, being based on the anatomical examination of

numerous specimens of each species and a careful comparison of the relative value of the different features observed. Vesque has likewise contributed greatly towards the anatomical method in classification and has shown its value in a large number of orders. In recent years large numbers of papers on the systematic anatomy of various orders and tribes has been published, which, although many suffer very considerably from a one-sided treatment of the subject, have still served to extend our knowledge and to establish firmly the right of existence of the anatomical method in taxonomic botany. The fact of its adoption in the Natürliche Pflanzenfamilien alone speaks for the recognition of its importance.

The anatomical characters of the vegetative organs, and more especially those of the leaf, are known to undergo very considerable variation according to the habitat of the plant, and moreover, in different species, different characters will be subjected to this variation. Constancy of all features can only be expected in species, all the individuals of which live under absolutely uniform conditions, and this rarely occurs. It is therefore of the utmost importance to examine a number of specimens from localities diverging as widely in character as the distribution of the species allows of, before any special anatomical feature is taken as characteristic of the species in question. Further, it must not be overlooked, that, just as the external morphology often affords few points for the distinction of closely related species, their anatomy may also be so similar as to render a separation on its grounds unfeasible. In no case can we depend on anatomy alone in generic and specific distinction, but if we take it hand-in-hand with the external characters we shall very frequently find that the two supplement one another in a most agreeable manner. Whoever endeavours to classify on anatomical characters alone will meet with greater difficulties than the purely morphological systematist of the old school. A truly scientific classification can moreover only be based on a complete knowledge of all the structural features of the plant.

One of the greatest objections that has been made to the anatomical method is the length of time involved in the determinal tion of a plant by its means. As a matter of fact, however, the time required is not or very little greater than that usually taken in the dissection of a flower; in most cases a surface section from the upper and lower sides of the leaf and a transverse and rough longitudinal section of a branch, all of which with some little practice can be

made in a couple of minutes, will suffice to show the main characters. Even a transverse section of the leaf, and radial and tangential longitudinal sections of the branch, which are requisite for a detailed examination in more complicated cases, are very readily prepared. A further objection to this method of plant-determination is the extremely imperfect state of our knowledge of the anatomy of many orders and genera, so that an anatomical examination of a plant is in many cases futile. There is no answer to this objection, but a method for its gradual elimination may be suggested. Every month brings the publication of large numbers of new species and in very few cases is their anatomy thought worthy of mention. It would be no such great increase of labour to examine and briefly describe the anatomy of each, and if the same thing were to be done in the case of revisions or discussions of earlier species, such as are frequently published, we should slowly but surely move on the way towards the universal use of anatomy in systematic botany. One of the chief drawbacks of such a mode of procedure would undoubtedly be the lengthening of the diagnosis, owing to the addition of the anatomical descriptions; I hope however shortly to be abie to propound a scheme of anatomical formulae to be used in such descriptions, which would reduce the additional space required to a minimum. Although in the preceding lines an attempt has been made to meet the objections generally brought forward against the anatomical method, there is no intention of acknowledging their right of existence, since the one aim in botany should be to elucidate all the features of a plant's structure, however great the labour and difficulties may be.

Within the limits of this article it is impossible to enter into a detailed discussion of all the anatomical characters of the plant, and a general account of the relative value of the different features must suffice. Many of the anatomical papers published have been confined to an examination of the leaf and stem, or even of the former only; for investigations of this kind, in which as many species as possible must be examined, are necessarily to a great extent confined to herbarium material, and the examination of the petiolar structure has been frequently omitted owing to the removal of the entire leaf, which it involves, damaging the specimen. In most herbaria however loose leaves will be found on one or the other of the sheets of the species and even if this is not the case the removal of a single leaf will mostly do little harm to the specimen. However it is the frequent omission of the examination

of the stem-anatomy, that is most to be condemned, for this, as being less subject to variation owing to external conditions, may be expected to afford generic characters in many cases, whilst the structural features of leaf and petiole are commonly only of specific value. Finally from certain observations it seems very probable to me that the anatomical structure of the fruit will not rarely be found to be of considerable importance in systematic diagnosis. An examination of the structure of the root is of course mostly impracticable from this point of view, besides being of a very uniform nature in most cases. The necessity of collecting spirit-material of new species wherever possible cannot be sufficiently emphasised; and it might further be suggested that the large botanical establishments, concerned with systematic botany, should keep slides illustrative of the anatomy of species examined, in order to facilitate future reference.

The anatomical characters of a plant have either been acquired in the remote past and handed down from generation to generation or are relatively recently acquired. The former are to a great extent constant and characteristic of larger groups of affinity, which are all derived from one ancestor, possessing those characters, whilst the latter are more subject to variation, and are frequently only of specific value; the former indicate the affinity, whilst the latter give rise to the structural differences in an allied group of plants. The former are naturally also characters which are little dependent on the external conditions. We must imagine the ancestor of each allied group of plants to have possessed the constant characters of this group and in addition to these, certain characters, more subject to variation—either internal or owing to the influence of external conditions—which have led to the formation of new species, etc., within the group.

Turning first to the structure of the axis, which seems most important for the characterisation of larger groups of affinity, pith, wood and cortex all yield excellent characters. In the case of the pith we have to distinguish between a homogeneous one, consisting of starch-containing cells alone, or of dead and empty cells alone, and a heterogeneous one, composed of both kinds of cells; these three features are not rarely characteristic of entire genera or even larger systematic groups, but will generally be found to be accompanied by more pronounced characters in wood or cortex, so that they are mostly only of supplementary value. The wood, as was first convincingly shown by Solereder (1885), affords a considerable

number of important points: the perforation of the vessels whether simple or scalariform, must be named first, the former character especially being constant for many orders, whilst scalariform perforations are characteristic of many genera, rarely of an entire order. The mode of perforation is evidently an inherent property of the plant—at least it is difficult to conceive of its dependence on external conditions—and must therefore necessarily be a feature of great systematic importance. The same is true of other characters of the wood, *i.e.*, the pitting of the wall of the vessels and of the fibres of the wood, and also the breadth of the medullary rays, but other features again—number and arrangement of the vessels, distribution and amount of the wood-parenchyma, shape of the cells of the medullary rays—will vary with the conditions of habitat, are only of specific value, and not even that if the species is capable of living in varying localities. The cortex, except for the one excellent feature, afforded by the point of origin of the cork, is subject to more variation within closely related groups than the other portions of the axis, The degree of development and the distribution of the fibres of the bast, of which much has been made by some investigators, is a character varying very much with the habitat; the fact that it affords a more or less constant feature in the Tiliaceae and some other orders, is probably due to similarity of conditions of life in the members of the order. These two factors, both of which cause constancy in anatomical structure, must always be kept in mind, *i.e.*, similarity of conditions of growth and the tendencies of the plant due to its ancestry; it will frequently be exceedingly difficult to separate the two, but where such a distinction can be drawn, the latter character should always be accepted as more applicable in the systematic characterisation of larger groups of affinity. Another feature of the cortex, which is undoubtedly also of great systematic importance, but must still be considered as dependent on external conditions, is the occurrence of a sclerenchymatous ring at the external limit of the primary bast (in the "pericyle" of Van Tieghem).

One of the most essential points of the structure of the axis in many orders still remains to be discussed and that is the occurrence of secretory organs. Although almost invariably also represented in the stem when they occur in the leaf, the reverse is not always true and thus an examination of the stem-anatomy is necessary for the determination of this all-important feature. Certain types of secretory organs—commonly with a definite kind

of secretion—are often constant throughout an entire order, whilst their distribution throughout the various tissues of the stem, as well as their shape, afford valuable characters for smaller groups within the limits of these orders; as examples it is sufficient to mention the mucilage-receptacles of the Tiliaceae and the resin-canals of the Anacardiaceae. The universal occurrence of laticiferous tissue in some orders has long been known and employed in characterising them, whilst Papaveraceae and Celastraceae show that even this character may be present or absent in closely related genera or even species. In spite of such exceptions (which may be due to a polyphyletic origin of the order), the occurrence of definite secretory organs must in my opinion be regarded as a character acquired long ago, although their distribution, shape, etc. is naturally variable with the conditions of habitat. The fact that the laticiferous elements for example are, in some orders, already differentiated at a very early stage in the embryo, indicates their phylogenetic importance and that they are not merely a recently acquired adaptive feature; far too little is known of the stages at which other types of secretory organ first appear, but a comparative study of this point would be most interesting.

The different features of the axis may be summarised, from the point of view of their systematic importance, in the following way:—

Characters usually generic or ordinal.	*Characters mostly only specific.*
Structure of pith.	Occurrence of isolated groups of sclerenchyma in pith and cortex.
Perforations of vessels.	Number and arrangement of vessels of wood.
Pitting of vessels and wood-fibres.	Distribution and amount of wood-parenchyma.
Breadth of medullary rays.	Distribution of secretory organs.
Cork-development.	Occurrence and arrangement of bast-fibres.
Type of secretory organs.	

With respect to the leaf the anatomical features of the petiole are largely dependent on those of the lamina, especially the distribution of the vascular tissue in the former, which varies considerably with the size of the leaf. As far as our present knowledge goes, petiolar characters are thus mostly only of specific value (but it seems likely that they may turn out very useful in this respect); however in the Dipterocarpeae they are constant throughout and the same is the case in the genera of Salicineae and Cupuliferae. The arrangement of the vascular system often presents marked differences in different

portions of the petiole, and it is advisable to examine a basal, a median and an apical transverse section in every case.

One of the most prominent features of the lamina and one which has long been employed by systematists, is the hairy covering. The constancy of a certain type of hair throughout entire orders (*e.g.* stellate hairs of Tiliaceae, two-armed hairs of Sapotaceae) is probably generally due to an inherent property in the plant owing to its ancestor or ancestors having had this kind of hair; under similar external conditions it is clearly retained, as in the majority of holopetalous Tiliaceae, whilst in the Sapotaceae, for example, a considerable amount of variation on the two-armed type occurs without its ever becoming absolutely obscured, *i.e.* this type is recognisable as the basis from which all the other forms of hairs found in the order have been derived. On the whole, however, the hairy covering, except in cases like the one just mentioned, in which all the hairs, occurring within the limits of an order, are reducible to one general type, is not a character of ordinal value, although of the utmost importance in specific or even generic distinction. Glandular hairs, as being more intimately connected with the physiological processes in the plant, which are probably almost identical in related groups, may be expected to afford far more constant characters, as is in fact the case. In the first place the mere fact of their occurrence or absence is generally a feature characteristic of entire orders, and then these external glands commonly preserve a very uniform type of structure throughout large groups, thus serving as a general character, rather than as a generic or specific one. The kind of mineral secretion (oxalate of lime, carbonate of lime, silica), as well as the form in which it occurs, is again undoubtedly of very considerable importance as an indication of affinity and for the diagnosis of genera or even orders, whereas the distribution and abundance of the same can rarely be even employed for specific distinction; in some cases the distribution has however been shown to be of some value, notably when one form of secretion occurs in the axis, whilst another appears in the leaf. The characteristic structure of the stomatal apparatus in many orders is undoubtedly due to an inherent property in the plant and is well-known to be of great importance in the characterisation of some orders (Rubiaceae, Cruciferae, etc.)

There are few other characters of the leaf that are of any great importance, although a number may in some cases serve for specific distinction. Of these we may mention the occurrence and

arrangement of groups of sclerenchyma in association with the vascular bundles in the leaf (sometimes of more than specific value), the structure and relative magnitude of palisade and spongy parenchyma (a very uncertain character in most cases), the degree of development and marking of the cuticle, the distribution of the stomata, the size and shape of the epidermal cells in surface view and the protrusion of epidermal cells into papillae; owing to the easy determination of this last feature it is often an excellent specific character. The presence of hypoderm and its structure, as well as the transcurrency or embedded character of the vascular bundles in the veins of the leaf (*i.e.*, vascular bundles of the veins either connected with both epidermes by means of strands of collenchyma or sclerenchyma, or embedded in the parenchyma of the leaf) are characters which are not rarely constant for larger groups of affinity.

From the phylogenetic point of view the structure of the seedlings is most important, as has been sufficiently shown by Miss Sargant's recent work on the Monocotyledons. In the seedling we may expect to find a very uniform type of structure throughout large groups and an examination of the same may in many cases make it possible to determine those characters of the adult plants which are due to their ancestral tendencies. At the same time the anatomy of the seedling may be expected to indicate affinities more clearly than that of any other part of the plant.

University College, London, F. E. Fritsch.
July, 1903.

ALTERNATION OF GENERATIONS IN THE DICTYOTACEÆ,

(Abstract of a Paper read before Section K of the British Association at Southport).

In the Dictyotaceæ the asexual cells are always borne on distinct plants from those that produce the sexual cells. The antheridia and oogonia may appear together on the same plants as in *Padina*, or on separate individuals as in *Dictyota*, but the tetrasporangia are never found on the same plants as the sexual cells. In view of this fact it is an interesting question whether the tetrasporic and gamete-bearing plants represent the sporophyte and gametophyte generations respectively, and whether they

regularly alternate with each other. The cytological evidence seems to prove conclusively that they do. If the vegetative cells of tetrasporic plants of *Dictyota* or *Padina* be compared with similar cells of the sexual plants, the dividing nuclei of the former are found to have twice as many chromosomes as those of the latter. In the stalk-cell division of the tetrasporangium there are thirty-two curved, rod-like chromosomes and the division is homotype in character, but the next division has a long period of preparation, there is a distinct spirem thread and the synapsis which usually accompanies the reduction stage, and when the mitotic figure is formed there are sixteen chromosomes which exhibit the characteristic forms of the heterotype division. The succeeding mitosis, which completes the formation of the four nuclei of the tetrasporangium, is of the usual homotype character with the reduced number of chromosomes. Mottier[1] has already described the reduction division and most of the other mitoses in the asexual plant, but he has not examined the cytology of the germinating spore or of the sexual plant. When the tetraspore germinates it is found that the reduced number persists in all the divisions.

In the male *Dictyota* plant the reduced number prevails in all the numerous divisions of the antheridium. In the oogonium there is only one mitosis, the one that cuts off the stalk-cell; here also the chromosomes are sixteen in number.

If liberated oospheres are left unfertilized they start dividing parthenogenetically, but after forming a few cells they invariably die. The figures formed in them are multipolar and show all kinds of irregularities of form, but the chromosomes always show the reduced number. The mitotic figures found in fertilized oospores, as might have been expected, always have the full number of chromosomes.

Here then we have a spore-bearing form whose somatic nuclei are characterized by the double number of chromosomes, while the gamete-bearing plant has the reduced number. The reduction stage moreover has all the characters that distinguish this stage in the higher plants. The inference is natural that the tetraspore germling with its reduced number of chromosomes will grow up into a sexual plant, while the fertilized oospore with its double number will produce an asexual plant; in other words there is true alternation of generations here.

It remains to prove this experimentally by cultivation from spore to spore. The numerous attempts made to this end have hitherto not been successful, owing to the difficulty of getting the plants to fruit in cultivation.

[1] Mottier. Ann. of Bot. XIV., 1900.

The reduction division, though similar in its main features to those of the higher plants, has some characters peculiar to itself. Among these is the fact that the spirem and the synapsis are very precocious, appearing while the tetrasporangium is still very small. After the longitudinal splitting of the thread there is a long period of growth of the cell during which the nucleus is apparently in the resting condition and the spirem as such has completely disappeared. In the prophase proper the sixteen chromosomes appear as long rods bent over so that their limbs are parallel, or cross each other, or meet so as to form closed loops. Detailed descriptions with figures are given in a paper shortly to appear in the *Annals of Botany*; here it only remains to add that the only explanation that seems to account satisfactorily for the facts is that suggested by Farmer and Moore, in their paper recently read before the Royal Society[1] in explanation of the phenomena of reduction in several plants and animals. According to this each chromosome is bivalent and only once split. The two arms of a looped figure would then represent two chromosomes, and the two are separated from each other by a transverse division during the metaphase of the succeeding mitosis, thus bringing about true reduction.

[1] Proc. Roy. Soc., Vol. 71, 1903.

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September, 1903.

THE COLONISATION OF A DRIED RIVER-BED.

By Marie C. Stopes, B.Sc.

(Read before Section K of the British Association at Southport).

IN the past the little river known as the Ebbsfleet, which ran from Southfleet to the Thames, just to the west of Northfleet, Kent, has had some influence on the history of the country. At its source was situated the Roman settlement of Vagniaci, and its presence interrupted the straight course of Watling Street. The stream was a stopping place for the pilgrims going to Canterbury in Chaucer's time, and there is proof that as late as Elizabeth's reign it was tidal, and of sufficient size for considerable ships to anchor on its course. This proves that the stream has a consecutive history of many centuries at least, but three years ago its water was abruptly and completely removed, thus leaving the water-loving plants suddenly exposed to dry conditions.

This is not the same, œcologically, as the slow drying up of pond or stream where the plants retreat generation after generation, and as I am unaware that any similar case has been treated botanically,

I venture to bring forward a few notes I have made upon it from time to time.

I had known the stream for many years, but took no specially botanical interest in it till the time of its destruction. I remember it, however, as having luxuriant growths of *Typha*, *Phragmites*, *Sparganium*, *Myosotis*, and many other water-loving plants along its banks; and thick tangles of *Potamogeton*, *Callitriche*, *Ranunculus aquatilis*, etc. floating on its surface.

It had a very winding course of about four miles through fields and marshy pasture land, and on one side there was a considerable plantation of willows.

The stream was about fifteen to twenty-five feet across, locally widening to forty feet and more, and had an uninterrupted flow of two to three feet of clear water coming from a perennial spring in the chalk. The supply of water was tapped in the winter and early spring of 1900-1 by the powerful pumps of a new waterworks, a couple of miles from the source, and by April, 1901, all water had ceased to flow. The thick mud at the bottom was thus exposed and slowly dried, till by July it was just firm enough to walk on. It was at this time closely intersected by large cracks, six inches or so across, and as much as three to four feet deep. At the bottom of these cracks I found dead eels and innumerable molluscs, but there was only the merest trace of blackened roots and scraps of stems from last year's vegetation.

At this time the mud was very largely bare of plants, particularly towards the middle of the stream where the last trickle of water had been, and remained uninhabited till September, when seedlings of *Nasturtium officinale* appeared, but did little that year. The rest of the mud supported a scattered vegetation, chiefly of seedlings, which grew in a very pretty way dotted over the bare mud. They varied much locally, but tended to grow in patches of almost "pure cultures" of *Juncus*, *Scrophularia*, grasses, etc.

There were only two true aquatics still growing, *viz.* *Ranunculus aquatilis var. trichophyllus* and *Lemna minor*. The *R. aquatilis* grew in considerable numbers under the shelter of the higher plants, sometimes in large patches and sometimes isolated. The seedlings were of entirely aquatic type, all the leaves being minutely divided, but they made very little progress throughout the year and were nearly the same size in October as they were in July, *i.e.* about two inches high; one plant only flowered, though the flower was of full size and entirely normal.

Lemna minor was growing near the edge of the stream bed, sheltered by willows and nettles; the plants were buried under an

inch or two of mud, but were green and healthy in appearance, and sprouting new fronds. They differed from the water-grown fronds in being somewhat fleshier, in appearing not to mind which way up they grew, and in having quite undeveloped roots. I kept this form in the laboratory for more than two months under similar conditions, but when they were placed in water they grew half-an-inch of root in four days.

These plants continued here till mid-summer, 1902, thus withstanding a period of dryness lasting nearly two years.

The growth of semi-aquatics was, on the whole, what one would expect, different plants dominating locally. They seemed to prefer the more exposed and lighter portions of the stream, while the sheltered spots were selected by land plants, specially *Urtica*. The total number of semi-aquatics that took any considerable hold was twenty, of which eight were locally dominant.

SEMI-AQUATICS.

Few.	Frequent.	
	Scattered.	Dominant locally.
Caltha palustris.	*Alisma plantago.*	*Carex paludosa.*
Carex hirta.	*Carex riparia.*	*Epilobium hirsutum.*
Eupatorium cannabinum.	*Digraphis arundinacea.*	*Glyceria aquatica.*
Juncus articulatus.	*Iris Pseud-acorus.*	*Helosciadium nodiflorum.*
J. obtusiflorus.	*Juncus communis.*	
	Ranunculus sceleratus.	*Myosotis palustris.*
	Rumex hydrolapathum.	*Nasturtium officinale.*
	Sparganium ramosum.	*Phragmites communis*
	Scrophularia aquatica.	*Salix sp.*
	Typha latifolia.	
	Veronica Anagallis.	
	V. Beccabunga.	

Total frequent—twenty, of which eight were locally dominant.

The dry conditions did not seem to affect seriously the growth of these plants, and a few of them, *e.g. Alisma* and *Myosotis* grew in far greater quantity than in any previous year. *Spiraea ulmaria*, although growing in great numbers on the bank, did not invade the stream at all.

All the plants flowered late, some not beginning to flower till September, but this was probably because very few had really a fair start till July.

Many of the plants were growing so as to shew that they had been distributed by the agency of the dwindling stream, the young plants only appearing down-stream in relation to the parents.

Of the plants encroaching from the land, eighteen had taken some considerable hold, of which five were locally dominant.

PLANTS ENCROACHING FROM LAND.

Few.	Considerable Numbers. Scattered.	Considerable Numbers. Dominant locally.
Asparagus officinalis. (1 plant).	*Anthoxanthum odoratum.*	*Chenopodium Bonus-Henricus.*
Convolvulus sepium (1.)	*Agrostis vulgaris.*	*C. alba.*
Dipsacus sylvestris.	*Bromus sterilis.*	*Equisetum palustre.*
Epilobium parviflorum.	*Glyceria distans.*	*Polygonum lapathifolium.*
Field Pea (1.)	*Holcus lanatus.*	*Urtica dioica.*
Papaver Rhœas (2.)	*Humulus Lupulus.*	
Phalaris canariensis (2.)	*Polygonum Hydropiper.*	
Prunus communis.	*P. persicaria.*	
Sonchus arvensis.	*Rumex conglomeratus.*	
Trifolium repens (2.)	*R. obtusifolius.*	
Vicia Cracca (1.)	*Solanum dulcamara.*	
	S. nigrum.	
	Tussilago Farfara.	

Many of them grew with unwonted luxuriance, notably the wild oat, which reached a height of seven feet, the flowering head being eighteen inches long. Also *Solanum nigium*, which Hooker describes as "having an erect stem six to twenty-four inches, rarely more" grew as large and straggling plants with stems four feet six inches long, and with very much the vegetative habit of *S. dulcamara*. These luxuriant growths seemed well accounted for by the original richness of the soil, the sufficiency of moisture, and the unusual warmth of the sun, but these very factors appear to have hindered many plants from growing there that one would have expected, *e.g. Papaver Rhœas*, many Composites and Leguminosae growing in the adjacent fields were almost unrepresented. Yet such Composites as *Leontodon* and *Sonchus* would appear to have had every chance of having their seeds scattered by the wind, and sticking to the damp mud.

There were also extremely few Leguminosae: I dug up all I could get, and found that *Trifolium repens* and *Vicia Cracca* had no tubercles developed, but that the field pea had exceptionally large ones, so the evidence was conflicting as to tubercle development in such a soil.

Another plant that appeared to have every opportunity of entering the new domain, and yet did not avail itself of it, was *Convolvulus sepium*. This grew in great quantity on one of the

river banks, right down to the old waters-edge and yet there appeared to be only one plant in the bed of the stream, and this did not flower.

The list of Bryophytes is exceedingly short, as was the life of most of them; it only comprises *Marchantia*, a small moss that never reached maturity, and *Funaria hygrometrica*. The Algæ were represented by *Vaucheria* and *Botrydium granulatum* on the mud, and *Cladophora* in a little pool near the spring.

I think this is rather remarkable, as there were seemingly such splendid opportunities for mosses and algæ on the sides of the deep cracks, which were quite moist, and protected from sun and wind.

At first there appeared to be but little struggle between the land plants and the water plants, there was plenty of room for each, for most individuals were solitary with considerable tracts of bare mud round them; for the water plants the struggle was against the adverse condition of being without water and exposed to sun and wind, and for the land plants it was primarily a test of dispersal and of suitability to the conditions. The distribution of the *Polygonum* is perhaps worth noting, as it was so diagrammatic at first. It always chose the exposed bank of the stream, as is seen from the diagram, where the dotted patches represent the growths of *Polygonum*, and the crosses, bushes or tall reeds Where a bush was on the exposed side, and so would afford shelter, it caused a gap in the growth at that place.

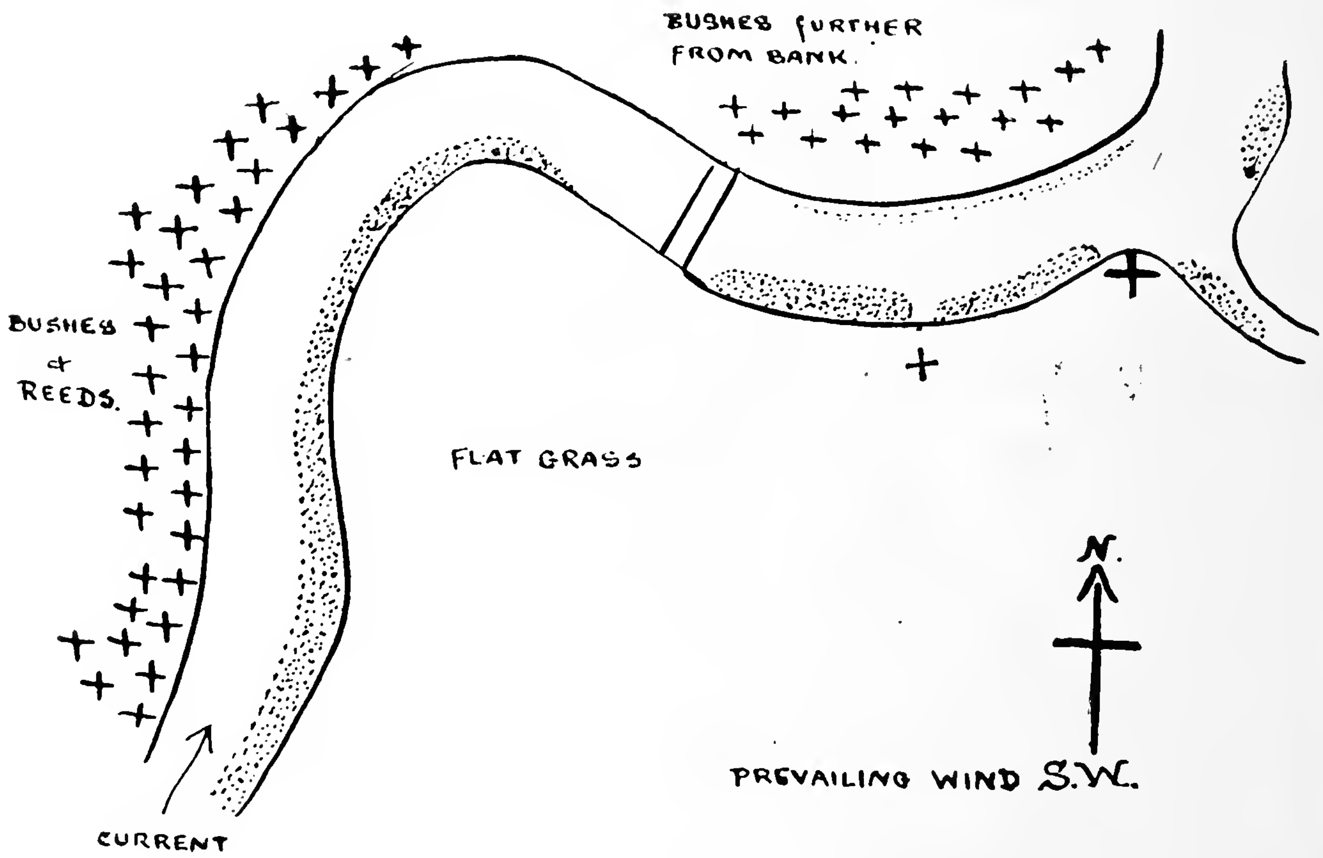

Fig. 1. Diagram illustrating distribution of *Polygonum lapathifolium* along sides of river-bed.

Later in the year the struggle between plant and plant began, and here it was often a case of the land plants against the water lovers, as *e.g.*, when a nice bed of *Juncus* seedlings was smothered out of existence by the rapid growths of *Polygonum*, or *Tussilago Farfara* overtopped *Alisma plantago*: but on the whole each had plenty of room, and the first year seems to have been a time when the plants were testing their powers against environment, rather than their strategy of warfare against each other. So that the lists given represent those plants which could grow and multiply on the drying mud of a river bottom.

By 1902 the physical conditions were increasingly hard for the water plants, and *Alisma plantago* and *R. aquatilis* succumbed; but *Spiraea ulmaria* began to make advances into the stream bed, and the others did not appear to suffer to any extent; *Scrophularia aquatica* being distinctly better than last year.

Lemna minor was still growing under the mud, green and apparently healthy.

The land plants were reinforced by *Bellis perennis*, *Sagina procumbens*, *Ranunculus acris* and a few others, but during the early part of the year they did not invade the territory secured by the water plants.

Leguminosae and Compositae, except for *Tussilago* and *Sonchus*, were still but slightly represented, while *Funaria* and *Vaucheria* both got considerable hold on the mud. The heavy rains of last year doubtless helped the water plants to hold their own, but towards the end of the year the land plants had largely increased.

There was very little bare mud left, except at the places which had been occupied by *Nasturtium officinale*, this plant appearing to leave the soil uninhabitable for some time after its death. The main portion of the stream was covered by thick jungle-like growths of *Phragmites*, *Typha*, *Sparganium*, *Epilobium*, nettles, grass, etc. in apparently lawless confusion.

Towards the source the stream-bed was composed of gravel lying directly on the chalk, and was without any muddy deposit. Here appeared a regular set of garden weeds, with no water plants at all, except *Scrophularia aquatica*, which was far more abundant this year than last, and even took to colonising heaps of rough flints.

In summarising 1902 I should say that it was a time of inextricable confusion, while the two associations of plants fought for the mastery, neither appearing to gain nor lose very much.

1903. The present year's heavy rains have undoubtedly prolonged the life of the water plants, but there are now only eleven

that retain any hold on the ground, of which the only ones that continue to dominate are *Glyceria aquatica*, *Phragmites communis* and *Scrophularia aquatica*.

Of the land plants we get thirty-two frequent, of which only three are Composites and none Leguminosae, and eight locally dominate, namely *Agrostis vulgaris*, *Chenopodium album*, *Holcus lanatus*, *Epilobium parviflorum*, *Galium aparine*, *Holcus lanatus*, *Humulus lupulus*, and *Tussilago Farfara*.

The land plants are now getting decidedly the best of it, except in a few places where *Scrophularia*, *Glyceria*, and *Phragmites* hold their own.

There are very mixed communities in which the land plants are usually uppermost, *e.g.* *Phragmites* and *Carex* are overgrown and nearly swamped by thick tangles of *Galium aparine;* the large hummocks of *Carex paludosa* that marked the edge of the stream form the foundation for knolls of *Humulus lupulus* and *Solanum dulcamara*.

Side by side *Phragmites* and *Urtica* are struggling for place, the *Urtica* frequently winning. The short turf that covers some areas is composed of a mixture of meadow grasses, *Helosciadium nodiflorum*, and *Veronica Beccabunga*. *Scrophularia* is fighting the grasses and winning, but the large areas that last year were blue with *Myosotis* are now inhabited by *Tussilago Farfara*, thistles and grass. Almost everywhere the doom of the water plants is apparent.

There are still many of the deep cracks, which collect rain water, and so long as they remain, so long will the water plants have some little chance. The farmers, however, have realised that there will never again be a river down that bed, and so they are adding it to their pasture land; and what with their attempts to form hedges, and the treading down of the vegetation by cows, horses and geese, it is no longer uninfluenced by man and his associates, and so has almost lost its original interest.

In this work certain points of interest come out about individual plants, but I much regret that I am scarcely able to give any broad and generalising results. This is largely because there is not a sufficient supply of streams despoiled of their water so conveniently for the botanist. If one could have a dozen to experiment on one could no doubt arrive at some generalisations. As it is I can only register the facts of this case, in the hope that others will arise with which they may be combined to form an addition to our knowledge of the adaptability of plants.

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ON STIMULUS AND MECHANISM AS FACTORS IN ORGANISATION.[1]

By J. Bretland Farmer, F.R.S.

I SUPPOSE it may be taken for granted that in the study of plants, as in other sciences, the ultimate aim of all enquiry is to establish a clear connection between cause and effect. The earlier stages in the enquiry consist in describing and classifying the effects or phenomena themselves, but there are probably few investigators who remain content with these efforts alone. In order to gain a wide comprehension of the phenomena it is essential that the factors that underly them shall be convertible into chemical and physical expressions, since in this way only is there any apparent chance of penetrating the temple in which the secrets of life are so securely guarded,

It must be confessed that most of the attempts in this direction have met with but scant measure of success. The hypotheses have often turned out to be erroneous and the theories destitute of any solid basis. But this circumstance does not affect the essence of the enquiry, nor indeed even its method. It is—or ought to be—a truism that the value of any hypothesis stands not in a necessarily direct relation to its final correctness, but rather depends upon the extent to which it welds together, even temporarily, cognate facts so as to suggest new lines of enquiry. No one doubts the value of the atomic theory, though of late there have not been wanting numerous assailants of this fundamental doctrine; and although perhaps few naturalists would be prepared to assert to-day with the same confidence that would have shown twenty years ago, that we have got to the bottom of the question as to the origin of species, nevertheless, history will assuredly preserve the great Darwinian Theory as one of the most precious landmarks in the advance of science and philosophy, whether it should ultimately turn out that

[1] A lecture delivered before Section K of the British Association, Southport, 1903.

its main outlines are to be permanent or not. It has paved the way for subsequent investigators and the fields thus opened up have proved rich indeed.

In a much more limited degree the efforts made to render the facts of organisation comprehensible have also borne fruit. But the ground is far less secure. The methods of analysis that can be utilised in statistical enquiries are less available here because the very factors that go to make up the whole are so dimly apprehended. Chemistry and physics at present render but relatively little assistance, and we have to trust largely to analogy, a notoriously unsafe guide. But unless we strive, notwithstanding, to express the results of our imperfect analysis in terms of things we can understand, we shall never make any advance at all. It is better to try, even if we fall into error, than to pass the whole subject by on the other side. A faulty and incomplete hypothesis is infinitely better than none at all, it at least awakes criticism, and everyone has plenty of the kind of friends who are anxious to detect and expose his errors. No harm, then, can come from an attempt to get a point of view—to deal hypothetically—I will not say theoretically, that would imply too much—with the main factors that determine those more obvious features of living beings that we call organisation and development. And in considering a matter of this kind, I do not propose to discuss critically the work of individual writers who have occupied themselves with this theme. The names of several will at once occur to you, and their views are not easily reconciled. *Quot homines tot sententiae ;* and it would be tedious to those unacquainted with the literature and superfluous for those that are, were I to attempt to deal with it. I will only therefore remind you that the various opinions are roughly divisible into two classes, the one depending on the assumption that there are formative stuffs present in the organism, that determine the production of its different parts, as root, shoot, and flower-forming stuff, and the like; while the other postulates the existence of a mysterious quality "polarity," and this property is regarded as determining the genesis and the appropriate distribution of the various parts.

Perhaps there is an element of truth in both of these views, but each one tested separately eludes one just at the critical point, and is apt to resolve itself merely into a round-about statement of the facts. The material theory invokes a *deus ex machinâ* that is difficult to grasp, whilst the second is too idealistic to admit of

detailed apprehension. Moreover a considerable body of facts are not easily reconciled with it. For if polarity really means anything it ought to be a definite and not a variable property; but the reversal of irritable properties (as for instance when the positive heliotropic character of a structure becomes changed into a negative response, or when the apex of a root turns into that of a shoot, as Goebel shewed might happen in *Anthurium*) seems opposed to explanations based on polarity as a working hypothesis. But although the analogies with simpler phenomena are difficult to accept as even approximate explanations of the facts; still if we cast a glance over the essential and more striking characteristics of living bodies, our attention is immediately arrested by certain salient and significant features. There is the property of specific form, and the equally remarkable one of the general occurence of symmetry, on which insistence has so often been laid in the past. But constancy of form would seem to imply that the constituent particles are held together by the *definite* and continuous operation of systems of forces the complexity of which may depend on the nature of the substance or substances involved, and the conclusion is enormously strengthened by considerations drawn from a study of symmetry and metamerism. One can hardly doubt that the units or metameres form closed systems, and that their form is, at least in part, the expression of the kind of matter of which they are made up.

In the inorganic world we know of simple substances that are capable—like sulphur—of exhibiting several crystalline forms, each depending perhaps on a different molecnlar arrangement, and we know too of many cases in which an infinitesimally small admixture of a foreign substance may effect the properties of the whole in important respects. In the world of living things it is not then to be wondered at that organisation is no simple matter. I need only refer to the deviations round a mean form, and the slight distortions of it, which at first sight seem so sharply to mark off organic shape from the definiteness characteristic of crystals. But we know of pseudo-crystals of organic substances in which there is not that degree of mathematical constancy that characterises such a substance as, *e.g.* common salt. Possibly the variability here depends on local variations in composition. But though the lability, semi-fluidity and other characters of an organism, perhaps, seem to forbid a comparison with crystalline form, I do not think we are unwarranted in seeking to find one.

The forms of crystals owe their origin and their properties (as

crystals) to the fact that their constituent particles—molecules or other aggregates,—are held together in systems by the operation of certain forces. That these take up more or less easily analysable geometrical forms probably depends on the homogenety and relative simplicity of the particles, but some *fluid* bodies are known in which nevertheless certain optical characters usually associated with crystalline structure are also met with.

But the *form* of a living organism, by the very fact of its constancy, can hardly be of a very different order, though the relationship of matter and force must be enormously more complex than they are in a crystal. And this materialistic conclusion, first I think seriously put forward by Herbert Spencer, is in harmony with the differences, as well as the similarities that mark diverse organisms. "All flesh is not the same flesh, but there is one kind of flesh of men, another flesh of beasts, another of fishes and another of birds," and it is just because they are not the same that the relationships that subsist between their constituent matter and the forces acting on it, find their expression in differences of form and of other properties.

I will not attempt to force an analogy between the similar crystalline forms often characteristic of salts of widely dlfferent composition and that mimicry of form so frequently to be observed in animals and plants. But I should like to say that the acceptance of the view that the form-character of an organism is an inherited property, the outcome of evolutionary changes, is no more an explanation of the phenomenon itself than it would be to assert that the crystals of salt deposited from a solution owe their form to the hereditary transmission of the form of the parent crystals employed to make the solution.

The *form* is transmitted in neither case, all that is handed on is the *material ;* and when placed under suitable conditions, out of the material arises—the necessary crystalline form in the one case, the necessary living form in the other, when the relations of force and matter are appropriately adjusted.

That the living form is immeasurably more complex is partly, perhaps largely, due to the continuously disturbing influence of those chemical changes that accompany the process of ontogeny, for in this way also the physical relationships of the parts concerned are as constantly being affected. But experience is against any assumption that this chemical march of events may be capricious in its course. On the contrary, in healthy life it pursues a fairly even,

albeit a complex track. When, however, it does become deranged we speedily observe indications of this in—*an alteration of form.* The alteration may be slight or it may be profound, and it may even affect the entire character of the organism. I need only mention a few examples to illustrate what I mean.

Galls, as is well-known, are due to the stimulus given by the presence of the larvæ of the gall-flies, and if these are killed the gall ceases to grow—the abnormal growth is certainly due partly to the existence of specific stimuli on the part of the animal, which not only can, but of necessity do, directly modify the normal sequences of events in the tissues affected, and so lead to growths that are characteristic mutually of the plant and the animal concerned. Different species, and in some cases different broods of the same species of gall flies, produce different kinds of galls, each one however specifically recognisable *per se.* The replacement of ovules by buds as the result of early infection by aphides is an example of a similar interference with normal processes by the addition of an abnormal stimulus of a material nature. Another remarkable example of form-change was discovered and elucidated by Dr. Blackman a couple of years ago; he found, by making incisions into leaves of cherry laurel, severed from the plant, that the leaves so treated cut out the wounded parts at *some distance* from the actual place of injury. The character of the excision is dependent on the nature of the wound and the circumstances of the environment, but the interest, in this connection, of the discovery lies in the fact that the stimulus has provoked new formative activities in the *living* tissues that are situated, it may be at a considerable distance from the actual seat of lesion. And once more, the familiar departure from its terrestrial or floating form assumed by the mycelium of *Mucor racemosus* when *immersed* in a nutritive medium affords yet another example, whilst finally I might quote the beautiful experiments of Klebs upon algæ, in which he shewed how closely the appearances of the various alternative phases and forms were bound up with the function of nutrition (in the widest sense of the term), and how regularly the plants could be induced to respond to altered stimuli by a definite physiological change of state.

Now although we possess at present very little precise knowledge as to the constitution of the more complex organic substances, rapid strides are being made in this direction, and I believe that the property of form will ultimately prove susceptible of intelligible analysis, and that just as in the case of many carbon compounds,

we can now confidently predict colour, explosiveness, and many other properties, from a knowledge of their chemical constitution, so we shall be able to explain the phenomena of symmetry, variations, and other form-relations, in very much simpler terms than are possible to-day.

I believe it is legitimate to draw a distinction between two sets of factors concerned in the production and maintenance of a living organism, the one is material, the other dynamical—put in this form probably no one would object, and left in this form I do not suppose the matter would be much advanced. But I think one may go even further, and regard the material basis as analogous to a mechanism, tuned to respond to certain stimuli in certain ways, the final character of each individual or each organ being the result of particular stimuli acting on particular kinds of mechanism. Chemical substances are precisely the same. A stimulus which will provoke one kind of response when acting on one material mechanism will provoke one of a different kind if it can affect a differently built machine. In endeavouring to translate these metaphors into something more directly similar to the things themselves, one is impressed with the fact that in the material substratum of a plant or of an animal we have to deal with vastly complex bodies, *diverse in different organisms*, capable of constantly undergoing change, as evidenced by growth and decay, disintegration and separation. These functions of metabolism are universally characteristic of living things and are associated with the protoplasmic body. And therein some unity of ground-plan seems to be indicated, and the clue is probably to be sought in the architectural conformation, that is in the chemical mechanism of the protoplasm itself, whether the units be termed biogens, micellae, or molecules. At any rate there is good reason for supposing the structure is highly complex, and that in some way a system that includes nitrogen within its boundaries is more or less loosely associated with one of carbohydrate-like structure. But the point is, that so long as the manifestation of vitality remains possible, the mechanism or arrangement is capable of being set in molecular motion and of undergoing certain more or less well-defined serial transformations when acted upon by appropriate stimuli. These changes may manifest themselves as physical, chemical or electrical disturbances, or in some combination of these. And although we are as yet unable to form any probably accurate guess as to the precise nature or character of the mechanism, nevertheless we can hardly escape the

inference that in some sort it has a real existence when we reflect upon the diverse results produced on different organisms or on different parts of the same organism, by relatively simple and identical stimuli, *e.g.* gravitation, or by the *change* in the character of response that may under appropriate conditions be induced in the organisation of many plants.

The term stimulus is an awkward one, for it is (at least implicitly) often used in two senses that do not necessarily correspond. The application of an external agent, such as light, may act indirectly as a stimulus, and its application be followed by a movement. But I take it this is often only a partial expression of the whole truth, and is perhaps a rather misleading part. The physically applied external stimulus serves to produce a change in the receptive sensitive structure, and here it is translated into an alteration of molecular condition and it is *this* that is propagated and finally excites the executive structure to perform the appropriate response. Whether the *response* be visible as a molar movement or not, it is pretty certainly invariably associated with some change in chemical structure.

Apart from a stimulus there can be no rearrangement of parts; no growth, no waste, no movement. It is conceivable that this inactivity might be induced in various ways. Either the proximate stimuli might be lacking, or the real ultimate stimuli, of which I have just spoken, might be unable to exist owing to lack of lability in the living substance itself, such as does happen, for example, when the watery contents fall below the minimum. We have such an instance in dried seeds that are capable of withstanding temperatures that under moister conditions would inevitably lead to the disruption of the vital complex of which the living substance is composed.

But given a stimulable condition, the particular result that will follow on any impulse will certainly depend on the nature of the mechanism affected, and it may also be modified by the kind of stimulus applied. In the latter case it perhaps depends upon the capacity of the transmitting zone to propagate different kinds of disturbances or decompositions when differently affected, in the alternative case any irritating agent can only affect this intermediate zone by setting up one kind of change. The optic nerve, however stimulated, only gives rise to the impression of light, and a Mimosa leaf makes the same response whether the proximate stimulating agency be a lighted match or a pair of forceps.

I cannot but think that this double aspect of the whole matter, the specific nature of the mechanism on the one hand, and the modes of excitation of it on the other have often been too little insisted on, and some at least of the confusion with which the subject of physiological morphology has become invested is to be attributed to this source. By applying this hypothesis of the combined result of the activating stimulus upon an actuated mechanism as a working hypothesis in endeavouring to gain a more comprehensive insight into the nature of the manifestation of vital activity I believe we shall be able to reduce to a common standard many things that seem at first sight to be only remotely related.

Take the case of the egg and the sperm. Each of these contains in itself the latent possibilities of a mature organism—but there is no evidence to shew that there is in them any microcosmic image of the adult; rather we are confronted with a substance out of which the mature form is gradually evolved in the sense of being built up out of the raw materials present in the germ. And this building up, that we call ontogenesis, is very clearly the result of a stimulus acting on a material characterised by considerable complexity of chemical composition. It is most significant that the more recent researches on fertilisation have clearly proved, not only that ontogeny is initiated by a stimulus, but that this stimulus need not necessarily be given by the act of fertilisation. Like the optic nerve, the structure of the egg is such that it responds to all agencies that can set its chemical machinery agog, in one way—by segmentation and development. As long as it appeared that fertilisation was a *sine quâ non* in the process, there was an element of mystery that seemed to baffle enquiry and elude comparison with simpler processes, but now that the various methods by which parthenogenetic development can be induced, whether by the action of certain salts, as in Loeb's experiments on echinoderm eggs, or by the disturbances produced on raising the temperature, as in Marsilea, or in any of the other ways known to us, it has become clearly apparent that anything capable of setting the machinery in motion may suffice to bring about development. The stimuli that continue to produce the further changes are equally clearly related to the internal decompositions going on in the mass of the young embryo, and again the influence of the mechanism becomes prominent in considering the effect of early artificial vivisection of its body. When the blastomeres are separated at their first formation, development in each is modified,

and small but perfect embryos may be produced. If on the other hand, the vivisection is a little deferred, till further stages of segmentation are reached imperfect embryos may result, the lost parts may or may not be replaced by regenerative processes that go on side by side, but not *pari passu*, with the progressive development of the mutilated embryo. The raw material for embryo formation may be all there, or at least be available, but the mechanism has been partly interfered with and its original co-ordination temporarily put in abeyance. Still more clearly is the same influence expressed in those numerous cases in which the structural parts of the young embryo are found to be correlated with the existence of specifically distinct zones or regions perceptible in the cytoplasm of the egg, any serious diminunition of which results, on fertilisation, in the growth of defective larvæ as is shown in the sea-urchin at an early period of its development, or in *Beroë* in the most adult stage. Other facts further pointing to the supreme importance of the egg regarded as a whole, as opposed to that of the individual blastomeres, when cleavage is artificially modified, all seem to point in the same direction. But nevertheless the *form*, that expression of the forces residing in and acting upon the material of which the labile mass is composed, is often ultimately and completely restored ; and when it is not, or when some new character (malformation or abortion) appears instead, this may be regarded as an indication that the serial changes that have gone on in the mass have induced a more or less profound change in the relations of mechanism and stimuli—probably both may be affected.

(To be concluded.)

REVIEW.

THE MORPHOLOGY OF ANGIOSPERMS.

THE scope of the book under review[1] is more easily appreciated than defined. The reader sees at once that it makes no attempt to cover the whole subject suggested by its title. It is a fair-sized octavo of 358 pages, and from these must be deducted about 70 which are most

[1] Morphology of Angiosperms (Morphology of Spermatophytes, Part II.), by John Merle Coulter, Ph D., Head of Department of Botany, the University of Chicago, and Charles James Chamberlain, Ph.D., Instructor in Botany, the University of Chicago. Pp. X and 348. New York. D. Appleton and Company, 1903.

usefully occupied by bibliography, index, plates, and the like. The page is not closely printed, there are very few foot-notes, and the text is reduced in bulk by the welcome introduction of many illustrations. Such a volume would be a miracle of compression if it presented a complete account of all that is now known concerning the Morphology of Angiosperms. But this is no examination manual, hateful alike to teachers and students: it is an eminently readable book with a distinct individuality, and its authors have achieved brevity by selection not compression.

The principle of selection is suggested in the Preface: indeed a phrase from the concluding paragraph might serve as a motto to the whole volume—"The final aim of morphology is a definite phylogeny." Accordingly the morphological characters chosen for treatment in detail are those which have yielded or are likely to yield evidence concerning the race-history of Angiosperms. The subject-matter of the treatise may be divided roughly under six heads: the origin and development of the gametophyte (Chaps. II.—VIII.), embryology (Chap. IX.), floral structure (Chaps. X.—XII.), geographical distribution (Chap. XIII.), geological history (Chap. XIV.), and finally the vegetative anatomy of the Angiospermous sporophyte as compared with that of the sporophyte among Gymnosperms (Chaps. XVI., XVII., by Professor E. C. Jeffrey).

The introductory chapter deals with two subjects: the separation of the Angiosperms from the Gymnosperms, and the internal division of the Angiosperms into Monocotyledons and Dicotyledons. On the former question the tendency of recent research has been to reveal the isolation of the Angiosperms at the same time that the connexion of Gymnosperms with Pteridophytes is demonstrated with increasing clearness. The authors give an admirable sketch of the evidence which has led to this change in botanical opinion, and they do not hesitate to draw the logical conclusion. "In our judgment...... Gymnosperms and Angiosperms should be recognized as two groups co-ordinate with Pteridophytes and Bryophytes. In fact Pteridophytes and Gymnosperms together form a much more natural group than do Gymnosperms and Angiosperms;—" It is for this reason that "the present volume is issued not as Part II. of *Morphology of Spermatophytes* (Part I. dealing with Gymnosperms appeared in 1901), but as an independent volume entitled *Morphology of Angiosperms*."

The characters which separate Monocotyledons from Dicotyledons are described at some length in this first chapter, but their

phylogenetic value is discussed later in Chap. XV. which is in fact the conclusion of the book so far as Professors Coulter and Chamberlain are concerned. It will be more convenient here to treat all that relates to this subject together, whether found in the introductory and concluding chapters or incidentally in other parts of the book.

In the two chapters on the Anatomy of Vascular Plants added by Professor E. C. Jeffrey to complete the work, the author comes to a very definite conclusion which is best given in his own words. "In the present state of our knowledge we are apparently justified in considering the Monocotyledons to be a modern, strictly monophyletic, and specialized group, derived from the Dicotyledons or their parent stock, possibly by adaptation in the first instance to an amphibious mode of life."

This opinion involves four separate conclusions: (i.) that Monocotyledons and Dicotyledons are derived from a single ancestral stock: (ii.) that this stock is geologically modern: (iii.) that the distinctive characters of Monocotyledons are specialized, not primitive, or in other words that the common ancestor was either a Dicotyledon or a more primitive form which closely resembled one: (iv.) that the early Monocotyledons may have been evolved by adaptation to an aquatic habit.

No such definite expression of opinion on this subject is found in the body of the work. The common origin of Monocotyledons and Dicotyledons is treated as an open question by the joint authors, and the evidence on both sides is given with admirable fairness. In the opinion of the present writer the balance of the evidence cited is very much in favour of such an origin, but the summing up on p. 283, and again on p. 287, is decidedly against it. The authors, however, agree so far with Professor Jeffrey as to allow that if such common origin be assumed, the derivation of Monocotyledons from Dicotyledons is more probable than the reverse (p. 286 and again, p. 288). They express no opinion on the method of derivation.

The section which deals with the reproductive organs and the gametophyte (Chaps. II.—VIII.) is in some respects the most remarkable in the book. It includes the whole story of "double fertilization," a subject in which the literature—though dating from 1898 only—is so scattered that a resumé of results together with a full bibliography was greatly needed. But apart from this, most botanists will be surprised at the amount of work dealing with the

origin and development of the embryo-sac and of the pollen mother-cell which is recorded during the past seven years.

The authors show very good grounds for the belief—in which they follow Overton—that the mother-cell of tbe embryo-sac is morphologically a megaspore, and that where a single megaspore occurs it is the survivor of a primitive group of four (p. 75). Such groups are shown to occur in many Angiosperms, and they are in all probability homologous with the almost universal tetrad of microspores.

In dealing with structures so far reduced as the Angiospermous gametophyte, it is often difficult to define their limits with exactness. Strasburger first pointed out in 1894 that the reduced number of chromosomes in the karyokmetic division of their nuclei was characteristic—so far as was then known—of the gametophyte throughout the vegetable kingdom. Later work has confirmed this statement, though, owing to difficulties of observation, the bulk of evidence is still very small, and it follows logically that the male gametophyte of Angiosperms dates from the pollen mother-cell, and the female gametophyte from the mother-cell of the embryo-sac (p. 41). The male gametophyte is much reduced, but there can be no doubt that its development ends with the formation of the two generative nuclei.

It is not equally clear what structures represent the female gametophyte of Angiosperms. For the present the question is well described by the authors as a "morphological puzzle" (p. 3). Nothing could be better than the way in which this difficult problem is handled in Chaps. V., VII., and VIII. The main issue is, of course, the morphological interpretation of the endosperm, and the alternative views are presented here with perfect fairness, while the authors make no attempt to conceal their own preferences. One criticism is suggested by this discussion. In dealing with the question of triple fusion the authors lay some stress on instances in which the polar nuclei never meet, but divide independently to form endosperm nuclei. On reference to a previous paragraph (pp. 166-7) five cases are found and they are quoted without any qualification which might suggest that the embryo-sacs were not normal in other respects. But on looking up the references the reader finds that the structure of the embryo-sac is more or less abnormal in each of the five cases. In *Antennaria alpina* fertilization does not take place: the egg developes pathenogenetically. In *Balanophora* no fertilization occurs: the embryo is developed apogamously from the endosperm. *Helosis* in all probability resembles its near ally

Balanophora. In the aquatic genera *Lemna* and *Lemnocharis* the structures within the embryo-sac are greatly reduced, and fertilization has not been observed, though it probably occurs occasionally in *Lemna.* If the theoretical value of the triple nuclear fusion is to be discounted because in a few cases endosperm tissue can be formed without it, we ought to think less of the importance of the fusion of male and female elements in ordinary embryo-formation because a few instances of parthenogenesis have recently been well authenticated.

The chapter on the Embryo (IX., p. 187) is particularly valuable as so much has recently been published on the subject, and it is all included in this admirable account. Not less welcome is the very full bibliography. Here too, as in the preceding chapters, the illustrations are for the most part drawn from original sources. They are very largely reproduced from memoirs published under the direction of the authors.

The subject of classification, depending mainly on floral structure, is treated in the three succeeding chapters (X—XII.) The authors give a general sketch of Eichler's scheme as modified by Engler, which cannot fail to be valuable to those readers who have not studied systematic botany at first hand. One assumption, first expressed in an earlier chapter (p. 10), but underlying the whole argument in this section, will strike many botanists as somewhat sweeping. "The vast majority of simpler flowers are better regarded as primitive than as reduced forms." The authors add: "At present this is at least a valuable working hypothesis, for it coincides in general with the morphological and historical evidence concerning relationships as well as with the doctrine of evolution."

The doctrine of evolution undoubtedly reveals a general tendency to increasing complexity of structure brought about by increasing competition between organized forms. The competition among herbs for light, perhaps, first produced plants taller and more spreading than their neighbours, and in the end trees came into existence with all thedifferentiation of vegetative structure necessary to secure mechanical stability, a sufficient water supply, and so on. But this general advance is modified at every stage by two factors which make for simplicity. In the first place it may well happen that some structure which at first gave its happy possessor an advantage over his fellows is in the end beaten in the struggle for existence by a similar structure of improved pattern which performs the same functionwith less expenditure of material. This may be the reason

why the seeds of extinct trees are often more massive and of more complicated structure than the seeds of Gymnosperms, their nearest living allies. In the second place though the complex structure may prevail over the simpler one under the ordinary conditions of life, stations continually present themselves to which the simpler organism is better adapted. Thus the competition for light in tropical forests leads to trees of enormous height branching only near the top, and the day of herbaceous plants would seem to be over. But epiphytes and climbers establish themselves on the trees and often get the lion's share of light without needing so cumbrous a machinery to secure it.

In some cases primitive forms survive in such positions—the backwaters of Nature. Aquatic animals and plants are sometimes of more primitive structure than their allies on land, and this is commonly attributed to their remote ancestors having been driven into ponds and streams by the greater competition on shore. But epiphytes as a class are not primitive, and it is clear that the original flora of the tropical forest would have little chance of surviving on the tree-tops. Before trees of sufficient size to support them had been evolved in the fierce struggle for light, the primitive herbaceous flora would have been strangled for want of it. The epiphytic flora would probably spring from the seeds of herbaceous plants carried to the tree-tops from a distance by the wind or by birds, and though the conditions under which they live no doubt impose simplicity of structure, it is a simplicity gained by reduction of unnecessary parts.

Every flowering plant has an enormously long genealogy, and in each generation the tendency is for the improved offspring to replace the older parent type. Even in the havens just described the primitive type is always in danger of being crowded out by some more advanced form which has discovered how to adapt itself by reduction to a simpler life. The primitive type is lost for ever when it is extinct, but there are endless possibilities of reduction.

The writer cannot but think that in an advanced group such as the Angiosperms, the chances are very much in favour of reduction as against primitiveness when the unusual simplicity of an organ calls for explanation.

We learn from the Preface that the book thus imperfectly noticed is the outcome of University teaching. No greater proof could be given of the excellence of a University course than the appearance of a text-book founded on it which is at once fresh and thorough.

October, 1903. ETHEL SARGANT.

THE LONDON BOTANICAL SOCIETY.

THE October meeting of this Society was held on Friday. October 30th, at the Royal College of Science, at 4.15 p.m., Professor Oliver in the Chair.

Dr. Scott shewed some lantern-slides illustrating the germination of the spores within coal-measure fern-sporangia. Many of the details of germination, exactly resembling those of recent fern-spores, were extremely well shewn. The sporangia could not be definitely assigned to any known genus of coal-measure fern.

Mr. Boodle exhibited some striking results in the local production of anthocyanin in the leaves of *Rheum*. The red pigment was confined to certain areas of the leaf supplied by veins which had been accidentally severed. A similar result was obtained experimentally by dividing the midrib of the leaf of the Evening Primrose (*Œnothera biennis*) about the middle of its course, when the whole distal part of the leaf beyond the cut became coloured red, the leaf of course having been left on the plant. The effect was only obtained when the affected part was exposed to full daylight. Mr. Boodle found that the different varieties of *Œnothera* were not equally good for shewing the effect. The explanation suggested was that the interruption of the channel by which the carbohydrate products of assimilation are normally removed from the mesophyll caused an alteratlon of glucose or anallied substance into the pigment. This is in harmony with the work of Overton[1] in which the occurrence of anthocyanin was found to be associated with an increased sugar content; and with that of Linsbauer,[2] who concluded that in cases of mechanical wounding the red colouration can be traced to a lowering of the facility of conduction of certain plastic materials. Mr. Boodle is publishing an account of his results in the next number of this journal.

Professor Farmer suggested that it would be important to test the effect of different rays of the spectrum upon the production of the red colour under these circumstances.

Mr. Boodle also exhibited some specimens of the flowering shoots of the Hollyhock in which the basal leaves shewed a tendency to become branched, or even compound. He pointed out that in the allied Adansonieæ the leaves aer normally compound, and suggested that his observation might perhaps indicate an ancestral type with compound leaves.

[1] Jahrb. f. wiss. Bot. 1899.
[2] Oesterr. bot. Zeitung, 1901.

Mr. Worsdell exhibited an interesting case of hermaphroditism in the flowers of *Begonia*. The inferior ovary was more or less degraded, and in one case a probably carpellary superior outgrowth from the receptacle was present. A head of *Scabiosa atro-purpurea* with virescent ray-florets and a double head of *Chrysanthemum* were also exhibited.

Mr. W. G. Freeman, Superintendant of the Economic Collections at the Imperial Institute, read a paper on the Uses of a Museum of Economic Botany, which will be published in the next number of this journal. He exhibited an interesting series of specimens and photographs from the Museum of the Imperial Institute, by permission of the Director, illustrating among other things coffee-growing in the Malay Peninsula, with coffee berries in various states of preparation, sugar obtained from the sugar-palm *Arenga saccharifera*) and from the coco-nut palm, ad ammar-torch, various kinds of rattans, etc.

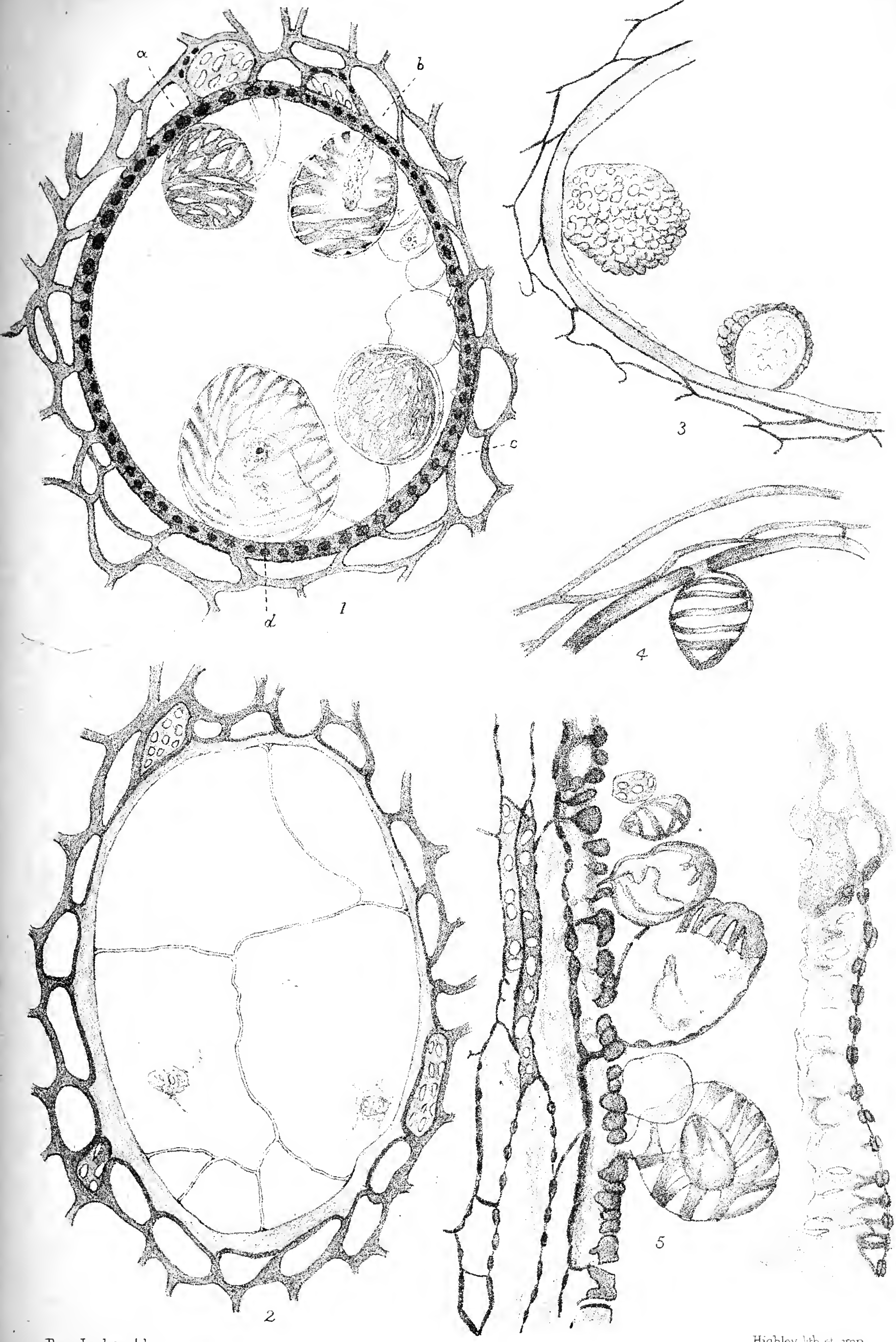
ON SOME PECULIAR TYLOSES IN *CUCUMIS SATIVUS*.

By Rose Jordan, B.Sc.

THE history of the occurrence and structure of tyloses was summed up in 1888 by Dr. Hans Molisch in his paper: "Zur Kenntniss der Thyllen, nebst Beobachtungen über Wundheilung in der Pflanze." Molisch describes the formation of both parenchymatous and sclerenchymatous tyloses, suggesting the various functions probably performed by these outgrowths into the xylem vessels of neighbouring parenchymatous cells.

He finds that as a rule woody stems give rise to tyloses with lignified walls, whereas in herbaceous plants thick-walled tyloses are of rarer occurrence. The sclerenchymatous tyloses figured by Molisch occur in the wood-vessels of *Piratinera guianensis* and *Mespilodaphne Sassafras*; they possess a narrow lumen and a thick lignified wall exhibiting very distinct concentric stratification. These tyloses completely fill the lumen of the vessel in which they occur and are connected with one another by pits.

In the herbaceous stems of *Cucurbita* and *Cucumis* the tyloses are usually thin-walled and may be found in two stages of development:—(i.) either as small outgrowths, more or less rounded, in the



Rose Jordan del.

Highley lith et imp.

Tyloses in Cucumis sativus.

vessel, or (ii.) of much larger size and pressed against one another, thus becoming polyhedral in shape and forming an apparently continuous parenchyma filling up the cavity of the vessel (Fig. 2).

Nuclei can often be observed in these cells. It is difficult to trace a connection between the separate cells of this tissue and the parenchymatous cells adjoining the vessel, but Molisch was able, by adding dilute chromic acid, partially to disintegrate the wall of the vessel and thus find the connection between the two, proving the tyloses to have arisen as out-growths from the neighbouring parenchymatous cells.

An exceptional case of tyloses, remarkable in so far that although found in an herbaceous stem the outgrowths have lignified walls, was found in a specimen of *Cucumis sativus*. In this specimen both forms of thin-walled tyloses already described were found to exist, the smaller ones often in the same vessels as the thick-walled form. The lignified tyloses remain oval in shape and never come together to form a continuous tissue as is so often the case with the unlignified tyloses.

In microtome sections a distinct connection can be traced between these thickened tyloses and the cells adjoining the vessel (Figs. 4 and 5), from which cells the tyloses have originated. The subsequent thickening prevents the tyloses from extending further into the vessel and they are never found to obstruct the passage completely. The lignified tyloses have pitted walls, the pits being either short and oval (Fig. 1, *a*, *c*), or long and narrow (Figs. 1. *b*, *d*, and 4) in which latter case they often approach a spiral arrangement (Fig. 4). The smaller pits are also met with in many of the adjoining cells of the wood parenchyma (Figs. 1, 2, 5), while the long narrow pits have only been observed in the tyloses themselves. In Fig. 1, a vessel is shown which contains in transverse section four thickened tyloses besides several normal ones ; the latter are smaller and might eventually become thickened like the others. *a* and *c* are seen in surface view, while *b*, and *d*, have been cut through medianly and show their contents,—contracted protoplasm and nucleus. This is a hand section and rather too thick to show the connection between the tyloses and the cells from which they are produced as is constantly observed in microtome sections.

A substance showing the reactions of "wound gum" is very often apparent both surrounding the tyloses and lining the vessel-wall. It is insoluble in sulphuric acid and caustic potash, does not swell up in water, stains brownish-violet with phloroglucin and

hydrochloric acid and stains like the lignin on adding aniline chloride, perhaps as Molisch suggests owing to inclusion of woody substances. Wound-gum is a substance constantly met with in connection with tyloses.

Fig. 3 represents part of a large vessel with two tyloses, both covered by this gummy substance which has the appearance of small rounded globules and renders the tyloses opaque. Between the two tyloses the inner wall of the vessel is also lined with the same gummy substance.

The presence of tyloses has often been considered as a pathological phenomenon or as a means of strengthening those vessels which are no longer required for conduction. On the other hand it has been suggested by Haberlandt[1] that the tyloses may have some direct connection with the flow of nutritive substances in the plant,—they may either store starch which can afterwards be transferred to the vessels, or they may extract certain substances from the transpiratory current which passes up the vessels. Certainly the tyloses increase the surface of contact between the vessels and the adjoining parenchymatous cells.

If they act as Haberlandt suggests and absorb food-substance from the vessels they would be comparable to the companion-cells of sieve-tubes, for like the companion-cells they would abstract material from the conducting elements and store it for further use, probably in their own vicinity. The material stored would not in that case be starch but raw sap. The thickened tyloses described in this paper would support the view that they may function as water-storage cells, for they are in structure not unlike the storage-tracheids (Speichertracheiden) mentioned by Haberlandt (Physiologische Pflanzenanatomie, page 355). These latter occur either as end cells of the vascular bundles, where they appear as somewhat swollen cells frequently having spirally thickened or pitted walls as in *Euphorbia Myrsinites*, or they may be transformed cells of the mesophyll. Spirally thickened water-storage cells occur also in the leaves and tubers of several epiphytic orchids and of *Nepenthes*. It is then quite possible that the function of the tyloses is to store up water containing food-substances and that the thickening of the walls is a protection against extreme variations of pressure, and would prevent the collapse of the cells when water is withdrawn from them.

If the comparison of tyloses with the companion cells of sieve-

[1] Physiologische Pflanzenanatomie, 1896, page 283.

tubes be adhered to, we might also compare the wound-gum found surrounding the tyloses to the callus blocking up the sieve-plates in the autumn. The purpose of the gum would then be to prevent the stored water from being withdrawn into the vessels in the autumn and it would thus retain the water for the use of those parts of the plant near which it is stored.

It has been impossible to confirm the suggestion put forward as to the function of the peculiar tyloses, as they were not observed until some time after the material had been collected in the ordinary way for laboratory purposes, and no further instance of such tyloses has been met with since then. Nor have we any information as to any special conditions which may have caused the production of these specialised tyloses.

Owens College.
July 31st, 1903.

EXPLANATION OF FIGURES ON PLATE X., ILLUSTRATING MISS JORDAN'S PAPER "ON SOME PECULIAR TYLOSES IN THE STEM OF *CUCUMIS SATIVUS*."

Fig. 1.—Transverse section of a large xylem vessel with pitted wall containing four lignified and pitted tyloses, *a*, *b*, *c*, *d* and several unlignified tyloses. The pitted walls of two wood parenchyma cells are shown.

Fig. 2.—Transverse section of a xylem vessel filled with thin-walled tyloses forming a pseudo-parenchymatous tissue. Three pitted wood parenchyma cells are shown.

Fig. 3.—Part of a xylem vessel in transverse section containing two tyloses covered by a gummy substance.

Fig. 4.—Transverse section showing the connection between a lignified and pitted tylose and a cell adjoining the vessel. The pits have the appearance of a spiral thickening.

Fig. 5.—Longitudinal section of a xylem vessel with pitted walls and the adjoining pitted wood parenchyma cells. The vessel contains five lignified and one thin-walled tylose and the connections between the tyloses and the cells from which they arise are clearly seen.

HONOURS AND POST-GRADUATE COURSES IN BOTANY AT THE UNIVERSITY OF LONDON.

THE reconstituted University of London is gradually developing its work on the important side of advanced teaching. Following on the institution of advanced courses in Physiology, held at the Physiological Laboratory of the University, the Board of Studies in Botany have recently arranged a three-year programme of similar courses in Botany, and have secured the services of eight lecturers to deliver nine courses of lectures, one for each term of this extended period. The Senate of the University have approved this programme and "appointed" the teachers in question. The courses are free.

The possibility of such a departure speaks well, we think, for the botanical activity of London at the present time.

The courses for the present session are "The Plant in Relation to the Soil" by Mr. A. D. Hall, Director of the Rothamstead Experimental Station, "The Lycopsida," by Dr. Scott, and "The Metabolic Processes of Plants," by Professor Reynolds Green.

Mr. Hall gave the first of his course of eight lectures, whose full title is "The Relation of the Composition of the Plant to the Soil in which it grows," at the Chelsea Physic Garden at 3 p.m. on Tuesday, October 13th. The lecture, which was attended by a considerable and most appreciative audience, and was mainly devoted to stating the problem of varying "quality" in different commercial crops of the same species or variety in scientific terms, and to showing that it is due far more to physical conditions of soil, water temperature, etc. than to the chemical constitution of the soil, was an admirable inauguration of the new scheme. The best thanks of the botanists of the University are due to the Committee of the Physic Garden for allowing the course to be held in the pleasant lecture room attached to the Garden. Professor Green's course will also be delivered at the Garden during the Third Term, while Dr. Scott's course, next term, is to be at University College.

Subsequent lecturers are Sir William Thiselton-Dyer, Mr. V. H. Blackman, Professor Farmer, Dr. Rendle, Professor Oliver and Mr. A. G. Tansley.

THE HOME COUNTIES NATURE-STUDY EXHIBITION.

"NATURE-STUDY" has "caught on," there can be no question of that. It may be sneered at by the superior person as a fad, but in scores of schools throughout the country, teachers are now busily engaged, each according to his or her lights, in trying to interest children in looking intelligently at natural objects, and in recording what they see in words and by pencil, brush or camera. That this is an enormous advance on the old state of things in which nature was either ignored, or so-called science was taught to children more or less by rote from frequently inaccurate text-books, can hardly be doubted. At the same time, as in the case of every form of activity which has the force of a popular "movement" behind it, the very enthusiasm with which it is taken up leads some of its devotees into mistaken paths.

The recent exhibition at Burlington Gardens was most interesting to the teacher of botany, as illustrating both the excellent work that can be done along "Nature-Study" lines and the dangers which beset the enthusiastic teacher.

The exhibition was organized by "The Middlesex Field Club and Nature-Study Society" and delegates from "The Selborne Society;" the exhibits all came from the Home Counties, taken in rather a wide sense. They came from all grades of educational institutions ranging from primary schools to institutions of the type of University Colleges, and included some from Field Clubs and from individuals interested in nature-study.

The first room was largely occupied by exhibits from primary schools. What can be done for quite tiny children in a London school by bringing natural objects to them was well illustrated by the exhibits from the Christ Church Endowed Infant School at Blackfriars. Various living animals such as a snake, a rat, a tortoise, etc., kept by the children in cases made by the staff, charts recording weather, wind, sun, etc., kept by the children, were shewn. Whether the so-called "co-relation schemes" in which a lesson on a natural object is illustrated by a picture, a story, a poem, etc., an attempt we suppose, to bring all the child's faculties into play in relation to the object, is a wise method, when the illustrations must necessarily often be rather third-rate, and the connexion not infrequently an artificial one, we leave the psychologist and the practical teacher of infants to discuss. In any case it hardly falls properly within the

scope of nature-study. The wisdom of trying to acquaint London children with the life-history and use of a wheat-crop by a series of most unlifelike models representing a wheatfield in its various stages, a mill, and a loaf of bread, may certainly be doubted. But there can be no doubt that the work as a whole is praiseworthy and good.

Sentimentality is a serious danger into which some teachers are clearly apt to fall. The photographs representing children in a school-garden, some of them working, perhaps, but one small girl unmistakably posing in a wheelbarrow, each photograph illustrated by a poetical quotation, irrelevant when it was not sentimental, were a particularly conspicuous instance. This kind of thing, if it has any effect at all, does children not good, but harm.

A great deal of the brush-work, in which a point is made of having no pencil outline, is quite excellent. We may mention that from the Invicta Road Board School, Blackheath, done by different children, mostly aged thirteen, and representing sprays of Chestnut, Beech, Oak, Rose, Nasturtium, etc., as extraordinarily good. The training in observation and artistic perception involved is worthy of great praise. At the same time mere brush-work, however good, rather falls short of "nature-study" in the sense in which it is generally understood.

Pen-and-ink sketches from nature of fruits and leaves, fleshy roots, etc., sent by another school illustrating lessons on these objects were very good, but against part of this exhibit we must emphatically protest. This consisted of sketches by children of twelve or thirteen representing microscopic sections of an ovule, of a liverwort thallus, and of a fern-frond with sporangia. In the first place there are such numbers of naked-eye objects over which children of that age can more usefully spend their time, that it is entirely unnecessary and probably undesirable for them to do any microscopic work. In the second place the sections from which these drawings were made were obviously bad sections, not illustrating the structure of the plants in question properly. And finally, such as they were, it is clear that they were not understood, for they were sprinkled with technical terms, largely wrongly applied; for instance a scale on the ventral surface of the liverwort was called a "multi-cellular rhizoid," and two layers of cells on the surface of the fern frond were called respectively "corky cells" and "palisade layer," while the structure of the ovule was completely misunderstood, not a single name being correctly applied. And yet to these sketches a

"first-class certificate and prize" were given, presumably by the school authorities! Clearly a rough-tongued inspector is wanted here.

Two other departures from legitimate nature-study may be mentioned. First some very finished water-colour drawings of a cultivated Chrysanthemum, a Pelargonium, and a Calceolaria, excellent perhaps as artistic products, but scarcely in place in this exhibition; and secondly some collections of dried grasses on card-board without any names or descriptions—things of little or no educational value, and including, by the way, plants which are not grasses. There were also a good many other collections of flowers with names attached, English and Latin, sometimes wrongly spelt, reminding one more of the "floral albums" of the middle of last century than of modern nature-study.

This hasty account of some of the primary school exhibits we are afraid contains a good deal more blame than praise. It was thought well to call attention to some of the dangers that should be avoided, but it must not be supposed that there was absent abundant and gratifying evidence of sound work on sound lines. Exhibits from Haslemere, from Peckham (including evidence of "long distance journeys" in pursuit of nature-study by teachers and scholars), from Bradfield, and from Dorking may be mentioned as examples.

In the secondary school section, there was much good work. Among this, the exhibits from the Clapham High School for Girls, and from Bedales School (Petersfield) were pre-eminent. In both of these the work in surveying and the principles of map-making, than which there is no more interesting and valuable exercise, shewed excellent results. At Clapham, among other things, the elementary physiology of plants is evidently taught in a simple but thoroughly effective manner, and the exhibit included demonstrations of the principal life-processes of plants with the aid of simple home-made apparatus, but all thoroughly workmanlike and adequate. The various exhibits from Bedales shewed that here also the pursuit of nature-study is carried on in a most varied and thoroughly en-lightened manner.

The geological maps and photographs from Tiffins' Boys' School, Kingston-on-Thames, constituted an excellent exhibit. This kind of work, giving an insight into the basis not only of scenery, but largely also of plant-distribution, might be much more wide-spread in country secondary schools. We must pass over a

number of other excellent exhibits in this section, noting that a certain number of the schools shewed a tendency to adhere to the less educational old-fashioned pursuits of mere collecting and naming specimens.

In the Section devoted to work in institutions of a higher grade, the Froebel Institute had a long series of exhibits, most of which were extremely good and interesting. Among these may be mentioned three very good collections of flowers to illustrate the characteristic floras of bog-country and moorland at different altitudes, of a mountain glen in Scotland, and of Margate, made during summer vacation, and all with explanatory accounts. There were also descriptions of an expedition to Hayes Common and Keston, with maps of the route embodying the results of the survey of the heath country, copses, bogs, ponds, etc., met with.

With regard to the general organization of the exhibition, it would have been more satisfactory if it had been found possible for the prizes to be awarded and the prize-winning exhibits marked *before* the exhibition was opened to the public, but we suppose this was hardly possible. We were sorry to see that the name of no recognised botanist appeared in the list of judges. This is particularly to be regretted since so large a proportion of the exhibits dealt with plants.

The promoters of the exhibition are to be warmly congratulated on its success, and on the stimulus it must have afforded to this most fascinating and important branch of modern education.

PERSONAL NOTE.

We are extremely glad to announce that Mr. L. Cockayne, one of the most enthusiastic of New Zealand botanists, whose excellent work on the native flora, particularly his observations and experiments on the youth-forms of New Zealand plants, we have for some time been intending to review, has been given an honorary Ph.D of the University af Munich.

R. Madley, Printer 151, Whitfield Street, W.

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ON STIMULUS AND MECHANISM AS FACTORS IN ORGANISATION.

BY J. BRETLAND FARMER, F.R.S.

(*Concluded from Page 201.*)

It cannot be too forcibly insisted on that life, *in its manifestations*, is ONLY recognisable as a series of responses to stimuli. Growth, one of the commonest phenomena, is clearly of this order. The stimuli are essentially given by the nutrition that is supplied to the growing parts, but here again the nature of the structure that will appear at any point as the result of a nutritional stimulus able to set the synthetic processes at work, will be determined not only by the stimulating substance, but also by the nature of the stimulated body at the time. Both are effective in producing the final result. One can hardly suppose that food-material, for example, flows upwards into shoots to settle there as *shoot-forming stuff;* or that root-forming stuff descends to the lower regions, in obedience with some geotropic sensitiveness, to make a root-forming mother liquor. How would it be possible on this hypothesis, to explain the formation of roots on the shaft of a Martagon lily while the postulated shoot-substance in this case flowed farther down to the bulbs and axillary buds. Or in the case of plants with creeping basal rhizomes, why do the roots and shoots, though all produced in the same zonal region of the stem, as in Circaea, still maintain their relative morphological positions in the tangle ?

But although there is strong evidence, from the phenomena of growth, that nutritive stimuli do serve as agencies for *provoking* development and increase in the number of parts in the higher plants, I believe there is no real evidence that they exceed this rôle. The actual form, the morphological nature, of the organ to be produced depends on the stimulated mechanism. Now in speaking of a mechanism, I am obliged to use this metaphor because I can not think of a better one, but I only mean by it a material

system that is capable under the conditions of its existence of causing substances to enter into new chemical and physical combinations. The mechanism itself is vastly complex, but it is thought of as owing its properties primarily to the manner in which its constituent elements and radicles are grouped together.

The outcome of its operations—the structural characters that will finally appear—depend for their existence on the character of the living substance having regard to *all the stimuli* to which it is at the time capable of reacting.

Thus Kny's experiments on cuttings planted upside down are of interest in this connection, and the old experiment of Sachs on the Yucca plant fall into line with them. On these reversed plant cuttings roots appear near the apical ends and shoots at the basal ones. The same result may be arrived at by pegging down the ends of blackberry runners, there root close to the apex, and by severing the rooted part of stem from the parent-plant, the buds behind the roots may be made to unfold, especially if the more apical ones be prevented from growing.

Now it is obvious in the above mentioned cases that the normal relation of the apical protoplasm to gravitation has been interfered with, but we can hardly omit to consider gravity as one set of stimuli that is known profoundly to influence the mechanism of the young formative protoplasm of stems and roots. If therefore we disturb this relation, is it to be expected that nutritional stimuli will go on producing the same effect as before? Is it not more reasonable to think that the alteration in the results of vital activity under the new conditions are in a large degree conditioned by consequent changes produced in the working of the mechanism itself, rather than in the direction of flow of specific organ forming-materials? I would refer in this connection to those physiological (and dependent morphological) changes that occur in the younger lateral shoots and roots when the "leader" or the tap-root may happen to be irretrievably injured but is functionally replaced by one or more of these lateral members.

Another remarkable series of phenomena are associated with growth. I mean the self-regulation of the structure of a plant as a whole. In this self-regulation is also involved the purposeful nature of the response to various stimuli. The latter point may be passed over for the present, but with the remarks that firstly as a matter of fact a large number of characters of any plant do not seem explicible on teleological grounds at all, *e.g.* the forms of many

simple leaves, whereas they do seem more easily intelligible on the material hypothesis previously outlined, and secondly those characters that do appear purposive, and the use of which is closely bound up with their form and distribution, may equally well be regarded as the expression of the necessary activity of internal factors; naturally only those species whose inner character expressed itself in making these "suitable" adjustments to the environment were able to survive.

The self-regulatory mechanism of plants, and indeed of animals also, at first sight may appear to be specially characteristic of living matter and to be far removed from chemical or physical treatment. A little consideration, however, will suffice to shew that so far from this being the case, this very quality affords a strong support to the notion that structure is the outcome of the operation of causes associated with the material constitution of the particular organism concerned.

The co ordination so often observed in the functional arrangements of an organ exists as the result of the appropriate chains or series of stimuli that of necessity originate when one part of the functional machinery is put into operation. The apparent co-operative action may be, in its net result, highly purposive, but to place this aspect of the matter in the foreground is to obscure the real significance of the sequence. For example, when a green leaf is engaged in the work of photosynthesis, some part of the soluble carbohydrate may perhaps diffuse out from the cell, but a considerable portion is temporarily changed with insoluble starch. Now since it is essential for its continuous production, that the excess of sugar should be removed and thereby prevented from arresting further synthetic activity, it is clear that its utilisation to form starch is a "purposive adaptation," a manifestation of the co-ordinated activity of the machinery, of the highest importance. But it would clearly be erroneous to say (as is often loosely done) that the starch is formed *in order that* more carbohydrate may be constructed. Experiment shews, at least in favorable cases, that sugar in sufficient amount is itself a stimulus to the plastids and can cause them to undergo those metabolic changes which result in the utilisation of the sugar, with a concurrent production of starch. It is inevitable that any organism that chanced to exhibit such a kind of mechanism would stand at an advantage, when competing with others from which it was lacking, and the same being true at any phylogenetic epoch in the history of the race, would lead to the

preservation of individuals possessing and retaining such mechanism in good working order.

I have mentioned galls as due to functional disturbances, that is to the existence of special relations between stimuli not normally met with in the proper limits of the plant-body and its responsive machinery, whereby out-growths having a definite form, due as I believe to the composition of their material substratum, are produced. And similar derangements are not unknown, though their causes are more obscure in animals. Tumours, and especially the malignant growths of cancer, are due to causes that unduly stimulate particular layers of tissue to excessive development, whereby they may proliferate and invade other parts of the body. Although at present the causes of cancer are obscure, we are very sure that if we can track the stimulating agency to its source, the secrets of the etiology of the disease will be revealed.

Allied to the problems presented by the facts of co-ordination are those involved in the processes of regeneration and healing of wounds. As regards the latter, a response to the action of the surrounding medium on the part of the protoplasmic body is a condition of its existence, and a lack of response would rapidly ensure the extinction of so imperfect a mechanism. It seems to be often thought, in the case of animals, that the inner organs of hypoblastic origin are less susceptible to reparation than those originating from the outer embryonic layers. May not this be an example of lack of response, because during the changes that have occurred in the gradually revolving organization, this property became less important as a criterion of the safety of the organism inasmuch as the tissues in question were less likely to receive those stimuli due to lesion ?[1]

It is the power of suitably responding to stimuli that in the long run determines the survival or extinction of a species, but the suitability or the reverse of the response is an *accident of the mechanism* as a working structure, and primarily is entirely independent of the causes to which the genesis of the mechanism itself is due. It is an out come of organisation, but in no sense the cause of it. The remarkable results obtained on extirpating the stalked eye of certain decapod crustaceans, whereby either an antenna-like structure or another eye may alternatively replace the lost part, according to whether the ganglion has been removed or not, emphasises this aspect of the matter.

[1] I do not attach much importance to this interpretation, and indeed the statement itself has been challenged.

A very significant feature in regeneration lies in the relation between the external form of the regenerated part and its internal structure. In plants, serious injury is often followed by the formation of a tissue which, in many of its properties, resembles that of the embryonic regions. Out of this new organs arise, and new tissues are differentiated, like those of the normal parts of the plant. But this resemblance is not always to be met with. Lizards, for example, easily lose and readily regenerate, their tails, but the new tail though similar in general appearance to the first one is by no means identical with it. This is seen especially in the internal structure. The bony axis, for example, is very different in the two cases. Clearly the stimuli and mechanism concerned are not the same as in the embryonic animal. The regeneration is not incomplete, it is divergent, although the general external lizard outline is reproduced.

The remarkable experiments on Salamanders by which double hands and other monstrous developments were produced in consequence of appropriate lesions of the arm may also be fitly cited here, as they provide still other examples of the effect of stimuli on mechanisms whereby under the conditions of the experiments, useless variants on the normal may result.

Those remarkable phenomena known as teratological are probably best to be brought under consideration here, though time will only permit of a brief glance at their more salient features. I have indicated that in galls we have a clear case of the production of specific forms as the result of stimuli given by known agents, though we are as yet entirely ignorant of the actual nature of the substance that produces the result, or even whether it comes, as is perhaps probable, from the glandular excretion of the larva The malformations that can be induced in roses by injudicious manuring is another case in point. But often we are unable to track even the proximate agent, and it is sometimes assumed that the character must be of the nature of a morphological reversion. I confess I find it difficult to think out how a plant can be supposed to replace such a structure as an ovule by a vegetative bud, or what not, *because these are "morphologically identical,"* for it does not replace the ovule by an ancestral type of shoot, but usually by one *bearing the character of the sporting plant itself.* Again, the seminiferous scale of a pine cone has been compared to the double needle leaves, or to a branch bearing these, but such dwarf-shoots are by no means characteristic of all conifers that exhibit double scales in their cones, as was long ago forcibly insisted on by Eichler.

When one comes to study those tissues that specially exhibit obviously irritable properties, one finds also strong evidence in favour of the association of a stimulus with a *material* change of the stimulated part, and also we learn that closely similar results may be produced in structures exhibiting widely diverse anatomical structure. Many tendrils are very irritable if touched in certain places, and the investigations of Haberlandt and others have shewn that in such cases special arrangements are often to be met with by which when they are touched, the protoplasm is deformed or squeezed.

Thus the stimulus is mechanically given in the first instance, but its initial effect on the *protoplasmic mechanism* is to produce a molecular change that results finally in a movement or change of form. In some cases it seems certain that the change works by altering the surface membranes of the protoplasts, thereby influencing the distribution of osmotic pressures in the affected tissue. Such is pretty certainly the case in such a plant as the Venus' Flytrap, when in consequence of an appropriate stimulus applied through the superficial hairs borne upon the upper surface of the leaves, the latter close up with such remarkable rapidity. The stimulus acts by causing a dimunition of turgor in the cells of the upper surface, and the now unbalanced turgid cells of the lower surface bring about the instantaneous closure of the leaf.

Similarly, in multicellular structures, the change of position produced by the one-sided action of light or gravity appears to occur through the influencing of the turgescence of the cells on the stimulated side, but the precise effect that will happen depends entirely on the nature of the stimulated mechanism. This is proved by the fact that the effect may even become reversed, as when a positively heliotropic organ becomes negatively heliotropic as it becomes older--a striking example of this is seen in the ivy-leaved toad-flax, in which the flowering pedicils are positively heliotropic, but later on, when the fruit is setting they bend away from the light. This can mean nothing more than that the material stimulable structure has undergone a change—for it is of course of no use to invoke a mere teleological explanation of the result. The process has its use, as far as the species is concerned (in effecting the sowing of the seeds), but the action itself is as independent of personal utility as is the gravitational attraction of two lumps of matter for each other. But the heliotropic phenomena of unicellular hyphæ of fungi shew that change in conditions of turgor is

not the sole means through which movements can be affected. For in them the mechanical conditions for a one-sided alteration of a turgescent system are wanting, and it seems certain that the stimulus provokes the action of a different kind of mechanism. It may be observed, in some cases at least, that the nuclei of the stimulated hyphæ become aggregated on the convex side of the filament, and perhaps this indicates some definite metabolic change by means of which the protoplasm is able to affect the elasticity of the cell-wall, further investigations are needed before this suggestion can be regarded as anything but merely tentative.

Many movements are observed to exhibit the pecularity of rhythm or periodicity, and this is specially the case with organs that are subject to intermittent stimulation. A remarkable example of induced rhythm has recently been described by Mr. Darwin, who exposed opposite surfaces of axial organs to periodically reversed stimuli given by gravitation. The result was that not only did a reversal of the movements accompany the changed conditions of stimulus; but this periodicity was observed to continue for a while after the application of the stimulus-reversals had been arrested. As the existence of rhythm is one of the most general, as well as perhaps one of the most remarkable facts associated with irritability, the subject urgently needs further investigations. May it be that the causes underlying it are correlated with those that also underlie growth? Certainly nutation is a very common rhythmical accompaniment of growth phenomena. Growth of a structure means rapid metabolism. We have direct evidence of this in the rapid changes that go on in the cells of actively growing zones, of stems and roots. Now the first action of a stimulus is certainly to modify metabolic relations. This in many cases is known to take the form of Katabolism, perhaps initially it always does so. But be this as it may, a local disturbance of metabolism means a corresponding disturbance of the energy relations of the system owing to the accumulation of chemical compounds of a more or less saturated character than those in the near vicinity. This may mean, if their diffusion is in any way opposed, or if its rate be relatively slow, that there is established a flow of nutriment or renovating material to the spot, followed by a reconstruction of the explosive material. Is it possible to imagine that there might be oscillations about the mean composition, due to self-distruction and subsequent renovation before relative uniformity is established after the discontinuance of the excitations? If the movement is

the outcome of chemical change, and I can find no other satisfactory hypothesis that will account for the facts, it would seem difficult to escape from some such conclusion, but whether it be correct or not it could probably be submitted to experimental test in a favourable case.

The relation of mechanism and stimuli may be considered in yet another connection, but I shall say very little about this, partly because I have already taxed your indulgence severely, and partly because the subject itself is so thorny a one, I mean the nature of variation.

The facts that have been brought to light within recent years seem to point to the conclusion that two quite separate processes have lurked under the common denomination of variation. There is the variation that can be induced in any given species by the modification of the environment. Examples will occur to everyone. Thus stature, spine-development, even leaf form, may vary immensely within the limits of a species and the variation may frequently be correlated with special conditions, *e.g.* moisture, light, or temperature. It would appear in these cases that one is dealing with a constant specific mechanism that is able to be actuated in different ways by different kinds of stimuli. But there is another kind of variation now familiar under the name of mutation in which the matter is apparently different. A mutant breeds true under conditions which ought to reduce it to the ancestral type if it belonged to the catagory of the variations I have just mentioned. But this does not appear to be the case. Moreover, one may find a species that is actually, so to speak, throwing off mutations, as for example the mutation type called *Œnothera lata*, which De Vries has repeatedly obtained from the common *Œnothera Lamarckiana*. The difference between such a form and the parental type seems to lie in a change of constitution which is only another way of implying a substantive change in the chemical mechanism.—And with a change in the mechanism, the *form*, that is the expression of a modified material constitution, cannot resemble in every respect that of the unaltered type from which it sprang.

Thus we might look on the first class of variations as the outcome of the operation of different stimuli on identical constitutions, whereas mutations would be recognised as the expression of the operation of identical stimuli on divergent constitutions. The strongest confirmation for such a view of the matter is perhaps that exhibited in the mosaic of hybrids. When the different sets of

characters severally diagnostic of the ancestors reappear, not as a blend of the two, but as segregated patterns, it seems impossible to escape the conviction that a segregation of material substance has correspondingly occurred, and that this, by virtue of its peculiar composition, expresses itself in a repetition of the respective parental forms, and the dominance of one parent, which may completely obscure the existence of the material substratum of the other, though this lies still latent within the body, is not opposed to, but rather falls in with such a material conception. And again the remarkable numerical relationships observed in those hybrids that conform to Mendel's rules, seem hardly explicable, save from the same standpoint.

In the foregoing attempt at a rough anaylsis of what I conceive to be the main factors that combine to produce organic form, I am far from pretending that much of what I have urged is novel, and I am fully aware that most of the rest is merely of the nature of hypothesis, but at least it seemed to me that another effort to try and realise how organic form may be regarded as a necessary outcome of the combination of matter and force, without reference to any teleological considerations of use or the reverse, might not be quite out of place, for current literature still teems with teleological explanations that really explain nothing, but rather bar the way of scientific enquiry. We may be, and probably are, far from the time when rigorous analysis of form shall be possible, but that such a time will come I have not the slightest doubt, and my conviction that the clue to the solution of the problems of organisation will be along the path of chemistry and physics must be the excuse for the tentative views, oftentimes vague as they are, that I have ventured to put before you to-day.

THE SEED CHARACTERS OF *PISUM SATIVUM*.

THE fact that the seed characters "round" and "wrinkled" in Peas are inherited in accordance with Mendel's law renders the histological nature of the difference between the two forms important. Microscopic examination of the seeds reveals a difference in the form of the reserves stored in the cotyledons of the two forms.

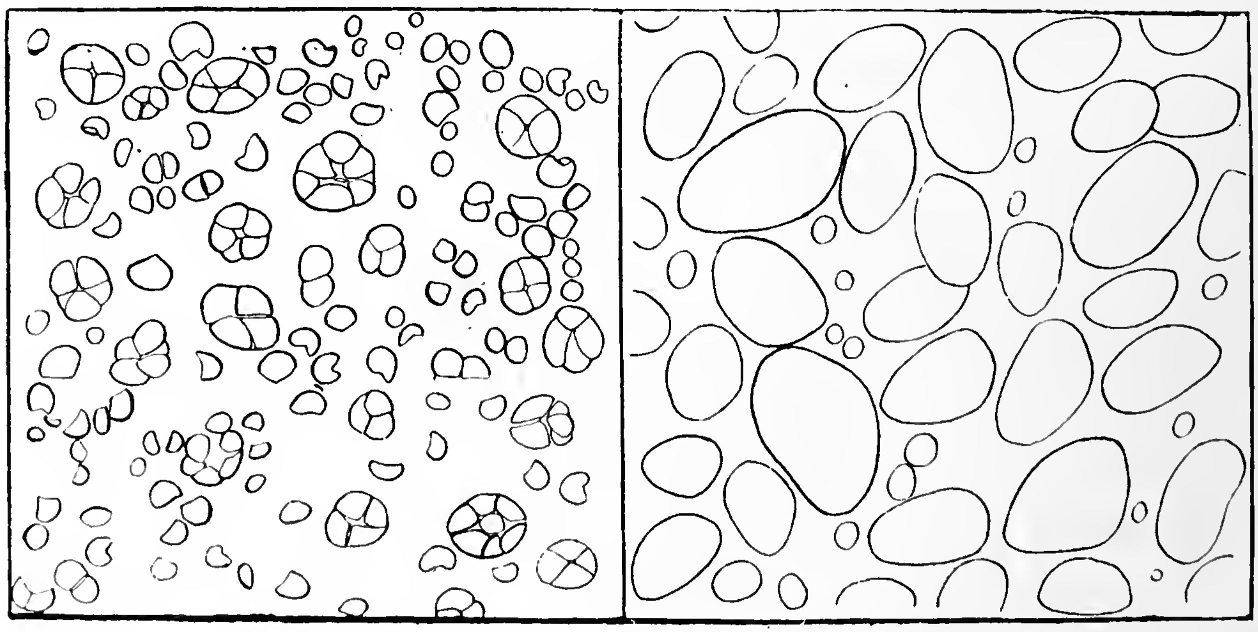
The starch occurs in grains of two very different and definite types, which can be distinguished at a glance.

In the *round* seeds the peripheral cell-layers of the cotyledons contain dense protoplasm with a few oval starch grains which do not exceed 0·06 mm. in their greatest dimension. In the third layer of cells the starch grains reach 0·2 mm. in length, while the more deeply situate cells are crowded with large oval starch grains measuring as much as 0·34 mm. in their greatest dimension. The grains are regular in shape, with a definite centre surrounded by well marked lines of stratification.

In the *wrinkled* peas the starch grains of the peripheral layers are of about the same size as those in the round peas, but are of a different type, occurring as irregular spheres with several centres, thus forming a compound grain which has a strong tendency to break up into smaller parts.

In the cells which lie more deeply, these compound grains reach a diameter of 0·18 mm. or rarely 0·2 mm. The component grains never attain a greater length than 0·1 mm. in their greatest dimension.

The accompanying figure will make clear the striking difference between the two forms of starch.



WRINKLED. ROUND AND INDENT.

Fig. 1. × 25. Starch Grains from Peas of the two types described.

The precise nature of the connexion between the form of the starch and the character of the seed as regards smoothness or the reverse is unknown. The wrinkled seeds, as compared with the round, possess a sensibly greater amount of cell-contents other than starch. Denaiffe[1] has observed that wrinkled seeds take up more water on germination than do the round seeds. Mr. Bateson's breeding experiments had led one to expect, however, that the "indented" types with coloured flowers would be found to possess reserves of the same type as the round seeds. This has proved to be the case.

The following is a list of the races the seeds of which, through the kindness of Mr. Bateson, I was enabled to examine:—

Race.	Seed Character.	Form of Starch.
Express	Round	Large
Fillbasket	,,	,,
Très nain de Bretagne	,,	,,
Maple (purple flowered)	,,	,,
Carter's Telegraph	,,	,,
Victoria Marrow	,,	,,
Field Pea (purple flowered)	Indent	,,
Purple Sugar Pea	,,	,,
Sutton's Purple-podded Pea	,,	,,
William the First	(see below)	,,
Telephone	Wrinkled	Small
Laxton's Alpha	,,	,,
Serpette nain blanc	,,	,,
Dark Jubilee		,,
Early Giant	,,	,,
British Queen	,,	,,
Windsor Castle	,,	,,

In certain races, seeds of intermediate or dubious shapes are not uncommon. The depressions in these seeds are sometimes mere *pitting*, as in Victoria Marrow, or they may be so marked that the seeds would be described as *wrinkled*. The latter are especially common in William the First. Microscopic examination showed at once that these seeds are really of the round type. There are therefore two entirely distinct forms of wrinkling; and while it is clear that the process by which the wrinkling is produced is connected with shrinkage on drying, the regularity of the shrinking in the round type, and its irregularity in the two other types cannot at present be explained.

[1] Les pois potagers, p. 9.

There occasionally occur among the offspring of hybrids between round and wrinkled types, seeds of a dubious shape which it is difficult on superficial examination to classify as round or wrinkled. Microscopically examined, each can be referred immediately, from the character of the starch grains, to the "round" or "wrinkled" type.

The existence of such seeds and types of dubious shape was taken by Professor Weldon[1] as indicating irregularities in Mendelian segregation or dominance. No seed has, however, been found which, upon histological examination, allowed of any doubt as to its true character. Consequently occasional pitting or spurious wrinkling must be distinguished from the true wrinkling of "wrinkled" types, and the shrinking which causes it must be the expression of a distinct physiological process.

R. P. GREGORY.

[1] Biometrika; Vol. I., 1902, p. 246, &c.

SOME OBJECTS AND USES OF A MUSEUM OF ECONOMIC BOTANY.[1]

By W. G. Freeman, B.Sc.,

Superintendent of the Colonial Collections, Imperial Institute.

ECONOMIC BOTANY is a broad subject whose scope it is not easy to state in a few words, but for practical purposes we may say that: Economic Botany comprises the study of the plants and plant products, which directly or indirectly are of service to man, including their source, distribution, collection and preparation, and their properties and uses.

The student of economic botany requires for the pursuit of these aims a thorough grasp of, at any rate, the general principles and important facts of systematic botany, vegetable anatomy and physiology, and of plant distribution; in addition he should possess a general knowledge of chemistry, physics, geology and zoology and would find an acquaintance with the principles of commerce and the use of statistics of service.

[1] Based on a paper read before the London Botanical Society on October 30th, the portions relating directly to exhibited specimens being omitted.

An instance of the economic value of systematic characters is afforded by the recent work of Baker and Smith,[1] who have demonstrated that there is a definite relationship between the venation of the leaves of many species of Eucalyptus and the chemical constituents of their essential oils.

The study of anatomical characters has solved questions as to the origin of several plant products, affords a means of detecting adulteration, and, for instance, in the case of Para rubber, has located the place of occurrence of the product in the plant and has led to improved methods of collection.

The economic applications of plant-physiology are so numerous that it is not necessary to refer to them in any detail. Scientific agriculture is practically applied vegetable physiology. The curing of tobacco, the alcoholic fermentation of sugar, etc., are instances of the economic uses of enzymes and yeasts, and in these and in similar industrial processes, improvements are dependent on advances in botanical knowledge.

Great results have been obtained in the past in plant breeding, and in the selection and raising of disease-resistant races, for instance of wheat and cotton. Progress in these fields is dependent on scientific research, possessing when it is carried out apparently little practical value. Thus the discovery of the factors which determine why one species, or certain individuals of one species, are susceptible to the attacks of a particular fungus, whilst another species or other individuals are resistant, would be of the greatest economic importance, although much of the work leading up to this result would be apparently devoid of any commercial value.

Chemical investigation is steadily being more and more resorted to as a reliable means of estimating the economic value of many drugs, tanning materials, rubbers etc., and it is common knowledge that the success or otherwise of many botanical industries, for example the manufacture of sugar, has been, in the main, dependent on the application of exact chemical knowledge of the processes involved.

Geological and climatic conditions, the geographical distribution of some harmful or beneficial animal, racial characteristics, rates of wages, to enumerate only a few items, are all important factors in the solution of many questions in economic botany.

[1] Baker and Smith. On the relation between the leaf venation and the presence of chemical constituents of the oils of the Eucalypts. (Proc. Roy. Soc., New South Wales, xxxv., pp. 116—123).

Nature of the Exhibits.

It might be thought sufficient to limit a museum of economic botany to a collection of the useful plants and their products, carefully named, and accompanied by notes on their properties and uses. Such a museum would undoubtedly have a certain value. Our aim should be much higher than this. We should show the product and its source, whether wild or cultivated, its occurrence or cultivation, collection and preparation for the market. Commercial samples of the final product, or of the manufactured articles should also be shown, accompanied whenever practicable by information as to the properties, availability, uses, etc. Full descriptive information should be given by means of concise, exact, simply worded, labels, and whenever possible photographs or other illustrations should be exhibited of the plant, and of any interesting stages in its cultivation, or in the collection and manufacture of the product. In addition there should be maps indicating its geographical distribution, and statistical data setting forth its importance. By the adoption of these measures the museum may be raised from the position of a mere exhibition to that of an educational instrument capable of imparting and extending scientific and commercial information respecting the economic products of the vegetable kingdom.

Arrangement of the Museum.

Having decided the general character of individual exhibits their mode of grouping next demands attention. This important question must, of necessity, be determined with due regard to the special requirements of those using the museum, and to the nature of the information attempted to be given.

The visitors to a museum of economic botany may be divided for our present purpose into four classes:—

(i.) Commercial men seeking information on the properties, uses, prices and availability of plant products from known sources; on new sources of, and possible substitutes for known products; and on the products and resources of certain countries.

(ii.) Botanists desirous of information concerning the economic uses of particular plants, or groups of plants, including their source, collection, properties, uses etc.

(iii.) Would-be emigrants and others interested in the economic products of special areas of the world.

(iv.) The general public interested in the source, manufacture and properties of objects of every day life, and to a greater or less extent in any of the above subjects.

Three possible modes of arrangement suggest themselves, all of which are employed in one or more important existing museums The grouping may be according to botanical origin, or according to uses, or according to country of origin.

(i.) The arrangement of vegetable products according to the systematic position of the plants yielding them, is a method of great interest to the botanist, as it shows him in the most graphic manner the relative importance of the various natural orders as the sources of economic products. He also appreciates the striking testimony afforded by the general uniformity in the character of the products and the properties of the plants of a single natural order to the value of the systematic characters employed in determining plant affinity.

The commercial man on the other hand is not usually interested in natural orders, and is handicapped by having to know the scientific name and natural order of the plant producing any product, the specimens of which he may wish to consult, unless, as in the case of Economic Museums of the Royal Gardens, Kew, assistance is afforded by a good series of descriptions and well-indexed catalogues. Having, however, located the position of the product, for instance coffee, he finds conveniently brought together all the specimens of it the museum contains, whatever may be their country of origin.

Although, as has already been indicated, many closely allied products, for example the fibres produced by plants of single orders as *Urticaceæ*, or *Liliaceæ*, are by this arrangement brought together fibres of distantly related orders are widely separated and cannot readily be compared. The arrangement also does not allow of information being easily gained of the products of various countries.

(ii.) The second method is to group the products according to their uses, the main divisions being food-stuffs, oils, gums and resins, rubbers, fibres, spices, timbers etc.; the sub-divisions being either geographical or botanical. At the Royal Gardens, Kew, the timber museum is arranged in this way with geographical subdivisions. This arrangement is also adopted in several of the important Colonial museums, and is undoubtedly of great practical value in any museum devoted to illustrating the products of a particular country. For a museum of more extended scope, there is much to be said in favour of this mode of arrangement. To the commercial man, or technical expert, desirous of examining and comparing fibres, or resins, or any other group of products, it

is certainly very convenient. He finds closely brought together all the specimens of each group the museum contains, whatever may be their botanical source or country of origin.

The method also allows of a good system of descriptive labelling. Thus taking some important product obtained from several countries, an account should be given of the plant and the conditions under which it grows. Its distribution should be shown on a map. A general description of cultivation and preparation would follow next, with notes on any exceptional methods employed in particular localities. Specimens of the product should be shown, accompanied by commercial information, and an account of their properties and uses. Statistical information, photographs, etc., should be introduced whenever possible. Such an exhibit would give a fairly complete summary of the known facts relating to the product.

The method has however some disadvantages. It is scarcely practicable to give detailed information respecting the climate, geology, economic conditions and other important facts of each country where the product is grown. Facilities are given to one group of commercial inquirers, but not to the second group—those desiring information on the products of particular countries. For the requirements of emigrants the arrangement is not suited.

(iii.) The remaining scheme of arrangement to be considered is the geographical, in which the products are grouped in the first instance according to their country of origin. This method is adopted in the Economic Collections of the Imperial Institute, the exhibits being grouped in Sections or Courts, arranged in geographical order. A sketch of the proposed arrangement of one Court, will serve to indicate the nature of the general scheme for the reorganization of these collections now being carried out under the direction of Professor Wyndham R. Dunstan, F.R.S., Director of the Imperial Institute, and at the same time to show the possibilities and limitations of the geographical mode of arrangement.

Each section should contain general, orographical, meterological and geological maps of the country. The distance of its ports from the principal markets of the world should be indicated.

Whenever available a map showing the distribution of the principal crops should be added, such maps being often of great importance in indicating a direct relationship between soil, rainfall or other conditions, and the area occupied by some particular crop.

Statistical tables should be employed to show the relative

importance of the chief products, the numbers of the various races comprising the population, and other facts of economic importance, The exhibits of each country should be grouped according to uses, the principal divisions being food-stuffs, timbers, gums and resins, drugs, etc. Each group should contain specimens both of products exported, and of products of value only for local use ; the exhibit of each product being arranged in accordance with the scheme detailed above.

Each section of such a museum would afford, when complete, a full representation of the products and resources of a particular country, and at the same time give information regarding the climatic, geological and economic conditions under which the products are produced.

For the commercial man seeking information respecting the products of certain countries, for the would-be emigrant and for the geographer this mode of arrangement is undoubtedly the most advantageous. On the other hand for purposes of examination and comparison of specimens of one product from different parts of the world the system is not so well adapted. Grouping according to use, and grouping according to geographical source are complementary systems ; they cannot be combined, and the advantages of one are the weaknesses of the other. For purely commercial purposes there are so many arguments to be urged for and against each of these systems that one cannot say that either is preferable under all circumstances. Much depends on the uses to which the museum is put in addition to that of pure commerce.

At the Imperial Institute an additonal collection of economic products from different parts of the Empire, is being gradually formed, arranged under subjects (fibres, rubbers, etc.), and comprising materials the composition of which has been determined in the Scientific and Technical Department of the Institute, and the uses, where not already known, determined by special technical trials conducted by manufacturers.

The geographical mode of arrangement has other interests. It brings out some of the general relationships between plants and climate in a striking manner. Anyone passing from section to section can scarcely fail to notice that whilst in the temperate climates wheat, barley and oats are the staple cereals, their place is taken in the tropical countries by rice and maize. Similarly the replacement of potatoes by sweet potatoes and yams, of the sugar-beet by the sugar-cane, to mention only two other instances will also be brought to notice,

A study of the products of some of the West Indian islands, in relation to the configuration, soil and climatology of the same islands, brings home in a striking manner some of the factors controlling botanic enterprise. Dominica, Grenada and Trinidad, for instance, are well-wooded, mountainous, and have sheltered valleys and a high rainfall; in these islands we find at the present time sugar of minor importance compared to cacao, limes, spices, etc. Barbados and Antigua, on the other hand, are comparatively treeless, open and exposed to the trade winds, and have a low rainfall; in these islands the cultivation of sugar is still the predominant industry, because although it is no longer so remunerative as formerly, there is no other staple crop (except perhaps cotton) to which the conditions are suited that can adequately take its place.

To sum up: A museum of economic botany should be devoted to illustrating the source, geographical distribution, collection, manufacture, properties and uses of vegetable products and the conditions controlling their production and utilization, the means employed being specimens, photographs, maps, descriptive information, commercial data, etc. The products may be grouped according to (1) their botanical relationships (2) their uses (3) their country of origin. In museums devoted to the products of only one country, the employment of the second method appears the most useful. In museums of a wider scope the adoption of the first method has a special interest for the botanist, the second and third methods appear of almost equal value for commercial purposes, the advantage being with the geographical system if the museum is extensively used to illustrate the products and resources of particular countries, and the conditions controlling botanical enterprise.

PROFESSOR JOHANNSEN'S EXPERIMENTS IN HEREDITY: A REVIEW.

BY G. UDNY YULE.

THE statistical theory of heredity, as developed in the work of Galton and Pearson, concerns itself with aggregates or groups of the population and not with single individuals. A number of laws have been formulated, on the basis of researches conducted in accordance with such theory, of which the most important is Galton's Law of Regression, *i.e.* the law that the offspring of abnormal parents are *on the average* less abnormal than such parents, "regressing" towards the mean of the race.

But the student of heredity, says Professor Johannsen[1] (p. 4), "cannot rest satisfied with such essentially statistical researches. A race, a population, an aggregate (Bestand) of any sort . . . . is by no means always, from the point of view of the biologist, to be treated as homogeneous (als Einheit), even when the individual variations are grouped round an average value, presumably "typical," in the manner expressed by the law of error. Such a population may . . . . . . contain a number of independent types (selbständige Typen), differing markedly from one another, which may not be discoverable at all by direct observation of the empirical frequency curve or table."

"Before such a population is treated as homogeneous" he continues (p. 5) "it should therefore be biologically analysed in order to be clear as to its elements, that is to have some knowledge as to the independent types (selbständige Typen) already existing in the population. Only after such an analysis is one in a position to decide whether, and how far, a treatment of the material as homogeneous is permissible. It is in fact such an analysis that Louis Leveque de Vilmorin had in mind when he . . . . . laid down his 'principle of isolation' . . . . . According to this principle one must decide by isolation—that is by keeping separate the seeds of each individual mother plant—whether the 'force héréditaire,' as Vilmorin terms it, be large or small."

[1] Ueber Erblichkeit in Populationen und in reinen Linien, ein Beitrag zur Beleuchtung schwebender Selektionsfragen: von W. Johannsen, Professor der Pflanzenphysiologie an der kgl. dänischen landw. Hochschule in Kopenhagen. Fischer, Jena 1903 (pp. 68).

These passages give the aim of Professor Johannsen's work, *viz.* the elucidation of the statistical laws of heredity for the race by the study of the corresponding laws for the "pure line," *i.e.* the posterity of a single self-fertilised individual. The results of three researches are given, the first two referring respectively to the weight and the length-breadth ratio of the seeds of *Phaseolus vulgaris*, the third to the phenomenon of relative sterility in barley as measured by the percentage of buds in a head failing to set seed. The barley used was a variety of three-rowed chevalier-barley.

For details the reader must of course refer to the original, but the method of the chief experiments may be illustrated by reference to those on the weight of beans. A single bean of known weight was taken, sown, the resulting plant allowed to self-fertilize (in a net-covered enclosure) and its seeds harvested. These seeds or a sample of them were sown in their turn, allowed to self-fertilize under similar conditions, and their seeds harvested. The mother seeds and their offspring were then weighed, and the results collected in the following form. (All weights are stated in milligrams).

LINE A.

Weight of the ancestral bean ca. 800.
Average weight of the mother-beans ca. 600.

Weight of the mother-beans.	Characters of the Offspring.		
	Average weight.	Number.	Standard deviation.
550—600	605	15	126·8
600—650	642	39	107·9
650—700	635	45	105·8
700—750	661	46	112·4
The whole line	641·9	145	109·5

Details are given for nineteen such "pure lines" as regards the weight of the beans and for twelve lines as regards the length-breadth ratio; the barley is treated in much less detail. The results are very simply summarised by dividing each set of "mother-beans" into two classes, "minus-variants" and "plus-variants," and expressing the mean weight of the offspring of each of these classes as a percentage of the mean of the line. The results for all the different lines can then be grouped together (Table 4, p. 37).

As regards the weight of the beans Professor Johannsen finds

Off-spring of the	
Minus variants	Plus variants
100.9	98·5

this result being based on 5494 seeds ; and as regards the length breadth ratio (2440 seeds)

Off-spring of the	
Minus variants	Plus variants
99·8	100 0

In short (p. 39) "the regression is complete, right back to the type of the line. The individual character of the mother-bean has no influence, nor has that of the grandmother, but the type of the line (der Typus der Linie)—of course in conjunction with the whole environment in the year concerned—determines the average character of the offspring." While "in some lines selection appears to be effective, in others the result is the reverse of what one would expect—on the whole nothing whatever is attained by the process of selection within the pure lines." The writer does not, of course, dispute the effective character of selection in an ordinary population, but in such a case (summary p. 58), "the work is carried out on impure material: the result depends on the more or less complete isolation of those lines whose types deviate in the required direction from the mean of the population....... And it will consequently be easily understood that the operation of selection cannot be carried beyond a certain limit—it must cease when the purification, the isolation, of the lines which deviate most strongly in the required direction is, practically speaking, complete." Later the author adds, to further emphasise the point (p. 64), "selection in a population is only effective in many cases in so far as it picks out the representatives of already existing types. These types are not formed in succession, *e.g.* by protection of those individuals that exhibit fluctuating variations in the required direction; they are simply found and isolated." These extracts give, I think, a fair idea of Professor Johannsen's position; but quotations removed from their context are never quite satisfactory, and I hope the reader will refer to the original.

The researches have been carried out on novel and carefully considered lines, and the results obtained are clearly of the highest importance for both practice and theory. As regards the former, they show conclusively that the breeder should proceed by noting the separate lines and not merely the offspring *en masse* of the individuals showing desired characteristics; by such a

procedure he will attain any desired end with greater certainty and speed. As regards the latter, the fact that heredity may be vanishingly small within the pure line, although quite sensible within the population at large is a very striking fact and, I believe, a new one. It must find its proper place and explanation in any complete theory of intraracial heredity.

Professor Johannsen's explanation, as I understand it, is this, that the race consists of a number of distinct "types," in each of which the germ-plasm structure (or whatever we choose to term the character of the germ cell that determines the character of the soma) is unalterable; that in a pure line all the variations are consequently *purely somatic* and therefore non-heritable; and that selection cannot operate in such a race because there are no germinal variations to afford the necessary material. On this hypothesis the heredity within the pure race is absolutely zero.

The hypothesis seems, however, to be somewhat qualified by later passages. The meaning of the word "Typus"[1] is not defined. I have assumed that the writer means an *unalterable* germinal structure, as it is only on such an assumption that the conclusions seem to follow. But on pp 61-62 of the summary, after a repetition of the statement to the effect that it is the "type of the line" in conjunction with the environment which determines the character of the offspring, and an approving quotation of De Vries's dictum that the line is "völlig konstant und höchst variabel" (germinally constant, I take it, and somatically variable) we read "Damit sei aber durchaus nicht gesagt, dass die reinen Linien absolut constant sein sollen."[2] In the first place, it is suggested,

[1] Statistically, the word is used in two quite distinct senses, neither carrying any implication of stability in the biological sense. (1) One may speak of the type of the race as regards any given character, meaning thereby the modal or most frequent value of the character (identical with the average, if, but only if, the frequency distribution be symmetrical). (2) One may speak of organisms "of a given type" within the race, meaning thereby simply organisms possessing a given value of the assigned character, within more or less narrow limits.

[2] I met with precisely the same difficulty in reading, some months ago, the very interesting work of Klebs on "Willkürliche Entwickelungsänderungen bei Pflanzen." On p. 145 is stated "Da wir von der Voraussetzung ausgehen, dass jeder Spezies eine konstante spezifische Struktur zu Grunde liegt . . . . ." while three pages later we find "Die Aufgabe der Speziesphysiologie ist aber noch aus einem zweiten Grunde grenzenlos weil die Konstanz der spezifischen Struktur . . . . . . doch nur relativ ist." The fact however that it is "relative" (*i.e.* really not constant at all) would have been better stated earlier. It limits many of the author's conclusions to an extent he does not realise.

continued selection for *many* generations may lead to an alteration of type, although selection for one generation only gives no sensible effect. "The burden of proof lies however with those who assume such an effect of selection." In the second place one must consider "Mutations, or the possibility of discontinuous variations of the type." "That they do occur" says Professor Johannsen, "appears to me beyond doubt." The latter statement seems to indicate that the writer does not consider the existence of mutations would invalidate his theory.

But, surely, the truth or otherwise of the hypothesis, that continuous selection within the pure race will ultimately affect the type, is quite independent of the *nature* of variation? If variations—germinal variations—in the required direction arise *in any way*, that is all that is needful. If *mutations* occur they will be picked out by the selector in the first instance, and the proportion of mutants to somatic variants will increase as the selection is repeated, because all (or a large proportion) of the offspring of the former will be retained and only a small (or smaller) proportion of the progeny of the latter. Is not the denial of the possibility of effecting a change of type, by selection within the pure race, a denial of the possibility of evolution itself? The existence or non-existence of the effect is not merely a criterion—nor a criterion at all—as to the nature of variation.

It seems difficult then, on very wide grounds, to admit that the effect of selection within a "pure line" or the intensity of heredity within such a line can be rigidly zero, *i.e.* the "burden of proof" lies with those who hold such a conception, which is inconsistent with the conception of evolution itself. All that can be proved by such experiments as Professor Johannsen's is that the effect is small (compared with the probable error of the result)—an interesting result, but a very different matter; for if the effect in given cases be not *zero* but only *small* it may in other cases be *sensible.* If Professor Johannsen believes in the occurrence of mutations he ought to believe in the effect of continued selection within the race, whether accepting the hypothesis of continuous variation or not.

It is unkind to "ask for more" where so much is already given, but one may point out that it would be of the highest value for comparative purposes to have data of similar form for a character more strongly inherited. Would it be possible, for instance, without making additional experiments, to regroup the material so as to deal not with the weight of the *single parental seed*, but

with the *average weight of the single seed on the parental plant* and the same character for the offspring? One would expect such a mode of grouping to give a greater intensity of heredity in the race at large and probably a sensible inheritance within the pure race.

The main question therefore seems to be this, are the results of Professor Johannsen's experiments consistent with the conception of continuous variation in the character of the germ-plasm? (That they are consistent with some form of discontinuous variation may, I think, be at once conceded). This question must be answered in the affirmative.

On the conception of continuous plasmic variation one may picture the formation of the germ cells of a pure race as accompanied by a process of gradual breaking up of the original germinal characters, controlled only by the action of selection (in the widest sense of that term). There must be a breaking-up of the original germinal characters (such as might be caused by the daughter cells receiving varying samples of the original germinal material), or no heritable variations would ever arise. There must be selection, or the breaking-up process would in course of time create variations deviating to an unlimited extent in every direction; which is absurd. Under the action of selection the process results in the genesis, from a single cell, of a series of somatic generations in which the variation gradually increases but asymptotes (provided all conditions are kept constant) towards a fixed limit. Under such circumstances the coefficient of correlation will also gradually increase and asymptote towards a fixed value, but the initial value and the ultimate value depend (1) on the intensity of selection (2) on the intensity of effect of circumstance—definite or indefinite—in producing *divergent* somatic characters from *similar* germ cells. The greater the selection, and the greater the divergence, the lower both the initial and ultimate values of the coefficient of correlation measuring the intensity of heredity.

To determine these two factors two independent data of some sort are needed, *e g.* the coefficients of correlation between mother and offspring, and between grandmother and offspring, in the ultimate race. Unfortunately no suitable data appear to be given by Professor Johannsen for the characters with which he deals. From two tables he gives (p. 16 and p. 42) one may however roughly estimate the coefficients of regression (for offspring on parents) for weight and length-breadth ratio of beans as about ·17 and ·23 respectively; the coefficients of correlation are probably slightly

less. Such low coefficients must mean a relatively very high effect of circumstance, and in such a case *the initial correlation between the daughters and grand-daughters of one mother must be exceedingly small* and the approach towards the ultimate value extremely slow. I have calculated the figures given below as a rough illustration of the sort of thing to be expected; the figures were obtained on the assumption of asexual propagation, which is not quite the same (on the continuous-variation hypothesis) as self-fertilization. The slowness of increase in the coefficient of correlation is possibly greater than that to be expected in Professor Johannsen's cases, as the ultimate coefficient (·117) is a little lower, but one cannot say for certain, not knowing the grand parental coefficient.

Table illustrating the gradual increase in the intensity of heredity between the successive generations of a pure line on the assumption of continuity ~~of~~ variation in the germ-plasm. The ancestor is reckoned as generation 0, and $r_{1\cdot2}$, $r_{2\cdot3}$, etc., are the coefficients of correlation between individuals of generation 1 and individuals of generation 2, between the latter and individuals of generation 3 and so on. s_1, s_2, s_3, etc. are the relative standard deviations of the successive generations.

$r_{1\cdot2}$	·0072	s_1	1000	$r_{11\cdot12}$	·0656	s_{11}	1032
$r_{2\cdot3}$	0143	s_2	1004	$r_{12\cdot13}$	·0698	s_{12}	1034
$r_{3\cdot4}$	·0211	s_3	1007	$r_{13\cdot14}$	·0738	s_{13}	1037
$r_{4\cdot5}$	·0276	s_4	1010	$r_{14\cdot15}$	·0774	s_{14}	1039
$r_{5\cdot6}$	·0340	s_5	1014	$r_{15\cdot16}$	·0809	s_{15}	1041
$r_{6\cdot7}$	·0400	s_6	1017	$r_{16\cdot17}$	·0840	s_{16}	1043
$r_{7\cdot8}$	·0457	s_7	1020	$r_{17\cdot18}$	·0869	s_{17}	1045
$r_{8\cdot9}$	·0511	s_8	1024	$r_{18\cdot19}$	·0896	s_{18}	1046
$r_{9\cdot10}$	·0563	s_9	1026	$r_{19\cdot20}$	·0920	s_{19}	1048
$r_{10\cdot11}$	·0611	s_{10}	1029	$r_{20\cdot21}$	·0943	s_{20}	1049

ultimate value of r	·1172
ultimate value of s	1064

Now the probable error of any correlation coefficient less than 0·2 or so is $\pm$ ·021 for a thousand observations, and the coefficient only reaches this value between the third and fourth generations. That is to say, if a thousand individuals (single beans) were gathered at each generation the correlation would only begin to be fairly well marked when the fourth generation of the "pure line" had been harvested. In many of Professor Johannsen's "pure lines" there were only two or three hundred seeds weighed; seven or eight generations might be grown before such numbers gave a clear result. The large effect of *definite* circumstances on plants (producing fluctuations not of the nature of errors of sampling at all) would further tend to obscure the results. The increase in variation, it should be noted would also be difficult to attest. The whole increase in twenty

generations is only 5%, and the probably error of a standard deviation (based on 1000 observations) is approximately 2%.

So far as they have gone then, Professor Johannsen's results do not seem in any way to contradict but rather to support the hypothesis of continuous variation. The results of succeeding generations will be awaited with a good deal of curiosity, if, as is to be hoped, the breeding of the "pure lines" is continued in such a way as to enable the above view as to the gradual approach towards the behaviour of an ordinary race to be tested; whether the view be confirmed or disproved it is equally desirable to have the experimental evidence.

Professor Johannsen's work is certainly one of the most important contributions to the theory of heredity of recent years, and his results should be studied and judged in the original by all who are interested in the subject. The mode of treatment is novel, and the study of "pure lines" a thoroughly sound procedure well calculated to elucidate the nature of intraracial heredity. One may add that the refreshing width of sympathy and sobriety of the author's style contribute not inconsiderably to the pleasure of the reader.

THE LONDON BOTANICAL SOCIETY.

THE November Meeting of this Society was held on Friday, November 20th, Mr. Percival being in the Chair.

Mrs. Scott exhibited the cinematograph camera which she uses in taking successive photographs of moving parts of plants, and explained her method of work. It was found that the ordinary cinematograph camera with a continuous series of films was unsuitable for the purpose. The type used had a large circular sensitive plate on which the photographs were taken in a spiral series. The greatest difficulty is the different exposures necessitated by the variations in the lighting of the object, since the series has to be spread over a considerable time. Another difficulty is keeping the object in the field, especially in the case of a growing shoot. That these and the numerous other technical difficulties met with had been to a large extent overcome was proved by the specimens of her work which Mrs. Scott shewed on the screen. Among the best of these was the series shewing the opening of the flowers of *Sparmannia africana*.

Miss Benson opened a discussion on the "Synangial Origin of the Seed," and brought forward a skilfully-marshalled series of facts and general considerations supporting the view that the Gymnospermous seed has originated from a synangium of which the peripheral members have become sterilised, the central one alone remaining fertile.

Professor Oliver, Dr. Scott and Mr. Worsdell took part in the discussion.

PERSONAL NOTES AND NEWS.

Dr. F. E. Fritsch has just returned from a twelve weeks' stay in Ceylon. He has been mainly engaged with a study of the conditions of life and distribution of the freshwater Algæ, some time having been spent in examining the Algæ of the mangrove swamps and river estuaries; these have proved to be of considerable interest. Plankton has been collected from a large number of different pieces of freshwater. Dr. Fritsch has also collected a large quantity of material of Hippocrateaceae and other orders of lactiferous plants.

Mr. R. H. Yapp, the Assistant-Curator of the University Herbarium at Cambridge has been appointed to the vacant Professorship of Botany at University College, Aberystwyth.

Mr. Boodle's paper on Anthocyanin which was announced for the present number of this journal will appear in a subsequent issue.

CORRESPONDENCE.

THE ORIGIN OF FLOWERING PLANTS.

DEAR SIR,

The question of the origin of Angiosperms—one of the most fascinating and difficult of botanical problems—has of late been revived as a fruitful subject for discussion and enquiry. I take this opportunity of calling attention to the neglect on the part of botanists of one of the most important forms of evidence bearing on this question. In attempting to obtain information in regard to the phylogeny of Monocotyledons and Dicotyledons, their common or separate origin, and the relationship which they bear to Gymnosperms or Pteridophytes, we must lay under contribution not merely the facts obtained by anatomical and embryological investigations of recent plants but extend our search for evidence into the records of the rocks. It is the latter class of evidence to which I wish to call attention.

In their recently published and excellent book on the Morphology of Angiosperms, Drs. Coulter and Chamberlain devote a chapter to the palæobotanical records of Flowering plants.[1] These authors, while commenting on the unsatisfactory nature of the available data, endeavour to give a summary of such testimony as we possess bearing on the phylogeny of the Angiosperms. The evidence is, I believe, even more unsatisfactory and less trustworthy than their treatment of it implies.

The most valuable palæobotanical discoveries made in recent years are those which are based on the study of petrified fragments of Palæozoic plants. Attention has therefore been concentrated on this branch of the Science. The less satisfactory and more difficult quest for evidence bearing on the ancestry of Angiosperms has, in consequence, been almost completely neglected. There are undoubtedly many serious difficulties to be considered in approaching the study of fossil Flowering plants; but we have spent our time in magnifying the unpromising features of the work instead of testing the capabilities of the available material.

The data quoted by Coulter and Chamberlain and by other writers have in many cases been compiled by authors whose lack of botanical knowledge renders their records of doubtful value, if not positively misleading and pernicious.

To quote one case: Drs. Coulter and Chamberlain refer to various Dicotyledons of Lower Cretaceous age, which it has been customary to refer to as Proangiosperms and to regard as comprehensive types. These so-called Proangiosperms are, I believe, in many instances of no botanical value and their designation by so alluring a title is not justified by the facts. Before we can hope to draw conclusions from fossil forms obtained from the oldest rocks in which undoubted Angiosperms occur, we must exercise the greatest care in sifting evidence and in eliminating all records that cannot be accepted with confidence.

My aim is not only to draw attention to the more or less worthless character of much of the material on which far-reaching conclusions have been founded, but to suggest that one of the most pressing needs is a thorough revision of fossil species from Cretaceous and Tertiary rocks. The work is laborious and extensive and beyond the power of the great majority of botanists to undertake single-handed. We require an organised exploration of the later plant-bearing strata and of the wealth of material already collected, which should be taken in hand by experienced palæobotanists in conjunction with botanists who possess a wide and accurate knowledge of recent Angiosperms. I am convinced that the study of fossil Flowering Plants is well worthy of attention, and if undertaken by men who well recognise the limitations both of the capabilities of the material and of their own unaided power of identifying fragmentary fossils, it is a study that will yield results of the greatest importance. It would not be difficult to obtain the assistance of experienced systematists to criticise determinations and to co-operate in the determination of species: a greater difficulty is to find workers who are willing to devote a considerable amount of time to a laborious task and to enlist the services of specialists in the determination of their material.

I have ventured to write this letter in the hope that it may be the means of obtaining suggestions as to how the critical examination of Cretaceous and Tertiary Angiosperms may best be undertaken.

Botanical Laboratory,

Cambridge,

Nov. 9th, 1903.

I am,

Yours faithfully,

A. C. SEWARD.

[1] Morphology of Angiosperms. J. M. Coulter and C. J. Chamberlain. Chapter XIV. (New York, 1903).

R. Madley, Printer, 151, Whitfield Street, W.